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JOURNAL OF PALEONTOLOGY

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PALEONTOLOGY

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DISTRIBUTION OF EVOLUTIONARY EXPLOSIONS IN GEOLOGIC TIME

A SYMPOSIUM

PALEONTOLOGICAL SOCIETY
SOCIETY OF VERTEBRATE PALEONTOLOGISTS
THE GEOLOGICAL SOCIETY OF AMERICA

at

El Paso, Texas
November 11, 1949

LLOYD G. HENBEST, *Editor*

Principal addresses

LLOYD G. HENBEST, JOHN P. MARBLE, G. ARTHUR COOPER AND ALWYN WILLIAMS, RAYMOND C. MOORE, CHARLES L. CAMP, GEORGE GAYLORD SIMPSON, AND NORMAN D. NEWELL

Discussion

M. K. ELIAS, CARL O. DUNBAR, JAMES S. WILLIAMS, RAYMOND C. MOORE, P. E. CLOUD, JR., KIRTLEY MATHER, PARKER TRASK, SIEMON W. MÜLLER, J. BROOKES KNIGHT, JOHN P. MARBLE, AND J. WYATT DURHAM

Chairmen

WINIFRED GOLDRING, C. L. GAZIN, and WENDELL WOODRING

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FOREWORD

WINIFRED GOLDRING
New York State Museum, Albany 1, N. Y.

IT HAS been deemed advisable to have the Chairman present the following explanatory statement:

In 1938 a program was held in the Paleontological Society of Washington on the distribution in time of the rise and fall of ancient groups of organisms. The discussion brought out information that cast doubt on the prevailing concepts of periodic diastrophism. The day after Dr. Gilluly's presidential address before the Geological Society in 1948, a symposium on the subject of the 1938 program was suggested for the Paleontological Society by Mr. Lloyd G. Henbest who had charge of the program mentioned. The response encouraged a formal proposal by him to the Council of the Paleontological Society, which approved and asked that he organize such a program for this meeting. The Society of Vertebrate Paleontologists was invited to participate and The Geological Society of America arranged for this to be a joint session of all three Societies.

The plan of the program is to present all of the papers in unbroken succession and to save the discussion until the last. The first paper, fittingly presented by Mr. Henbest, is intended to outline the scope of the problem and its significance for the methods of historical analysis in geology. Whereas the accuracy of geochronology is a basic issue in our discussion, Mr. John P. Marble, a leader in his field, was invited to outline the accuracy of age determination by radiogenic isotopes. The papers that follow will be given by noted specialists in paleontology, who have been asked to describe the "distribution of evolutionary explosions" with regard to their special studies and, in addition, to give their views on the meaning of their data for periodic diastrophism.

PRINCIPAL ADDRESSES

WINIFRED GOLDRING AND C. L. GAZIN, *Chairmen*

SIGNIFICANCE OF EVOLUTIONARY EXPLOSIONS FOR DIASTROPHIC DIVISION OF EARTH HISTORY—INTRODUCTION TO THE SYMPOSIUM[1]

LLOYD G. HENBEST
U. S. Geological Survey, Washington 25, D. C.

ABSTRACT—The purpose of this symposium is to examine the foundation in paleontology for the principle that diastrophism is the ultimate basis for dividing geologic history. The diastrophic theory maintains that crustal movements are periodic and synchronous on a world-wide scale, and that the segregation and conformity of biologic events with stratigraphic systems and series represents a primary basic connection between the processes of diastrophism and organic evolution. A close scrutiny of the "Distribution of evolutionary explosions in geologic time" provides significant if inconclusive evidence on whether organic evolution and crustal movements conform to the same world-wide rhythmic pattern or are more or less independent and provincial as to rate of change, duration, intensity, and amplitude.

Systems and series of rocks are separated in most places by stratigraphic breaks. The time spanned by these breaks and by the diastems within the systems and series commonly exceeds that recorded in the sediments of a geologic column. Inasmuch as fossil preservation is limited to the sediments in systems and series, limitations of the stratigraphic record are imposed on the records of the genera and species of organisms. The stratigraphic diastems and breaks impose corresponding "dark ages" on the fossil record. By projecting the evolutionary trends of genera and of evolutionary bursts into or through the dark ages at rates of change that are discernible in the preserved records, an evolutionary continuum emerges where a catastrophic pattern was imposed by the conditions of preservation. By this and other means of reconstructing the history of life during the dark ages, the rise and fall of groups of organisms are found to occur serially in tandem or in overlapping and complementary successions. Clear, simple connections of evolutionary history with so-called diastrophic rhythms are not supported by unambiguous evidence. A close examination of the accuracy of the stratigraphic, paleontologic, and radiogenic lead methods of geochronology shows that it is not yet possible to correlate crustal movements on opposite sides of the earth with sufficient accuracy to determine whether the movements conform to a world-wide pattern of rhythm and periodicity or are provincial. The dissimilarity between the systemic successions of rocks in the Southern and the Northern Hemispheres is devastating for the diastrophic theory.

PURPOSE

THE purpose of this symposium is to examine the foundation in paleontology for the diastrophic theory.

The diastrophic theory predicates that (1) diastrophism is periodic and synchronous on a world-wide scale; (2) diastrophism is a major control, if not the principal stimulus, of organic evolution; and therefore (3) diastrophism is the ultimate basis for correlating the events of earth history. This theory represents the prevailing concept in historical geology. Its tenets are widely accepted and taught even in their extreme form. In the last few years, however, there is a growing recognition that some, at least, of the tenets are artifacts of circular reasoning.

Even before Chamberlin (1909) recognized and explicitly formulated this concept in his diastrophic theory, it had been a guiding principle in paleontology and geology for many years. The concept offered a simple way of correlating and of classifying the staggering complex of geologic records. The idea has become so deeply ingrained in ge-

[1] Publication authorized by the Director, U. S. Geological Survey.

ology and stratigraphy that even those who doubt its truth, honor it inadvertently in practice.

Whether the diastrophic theory represents natural law, or half truth, or represents for geology the outstanding delusion of our age can not be determined without reexamining the methods of historical analysis of which it is a product. That is too broad a subject for a single symposium because the implications of the theory reach into every field of geology. The inquiry can be narrowed down, however, because the crux of our problem is chronologic. Whether crustal movements have taken place in world-wide, rhythmic pulses or at dissimilar rates and times must depend for proof on the quality of correlation and dating.

From the beginning of geology as a science, stratigraphic paleontology has served as the principal means of dating and of correlating the events recorded in the different and disconnected geologic provinces of the world. The accuracy of stratigraphic paleontology becomes, therefore, the central issue in our problem. The significance of this problem reaches into all divisions of geologic science. The very existence of geology and all of its branches as sciences depends on their competence to determine the relationship of events to each other in time. All considerations of cause and effect and of process and reality become meaningless without the dimension of time.

A difficulty that confronts an analysis of the correlation of systemic successions or of the orogenic movements with which they are connected is that the breaks between periods and systems and certain epochs and series appear to represent geological dark ages—times of disturbance or even of profound revolution. Various evidences agree in indicating that these dark ages and intervals of poor records represent large fractions of the time spanned by the stratigraphic sequences in each geologic province of the world. It is clear that we can not proceed far toward solving the central problems of this symposium without some clue as to the events of those times—whether they represent world-wide breaks or are but provincial interruptions in an evolutionary continuum.

The "Distribution of evolutionary explosions in geologic time" was chosen as the subject of this symposium because this subject bears on several basic aspects of the diastrophic theory. Evolutionary trends can often be projected across boundaries between geologic series, systems, or even eras. Abrupt first appearances of genera representing an advanced stage of evolution give clues to events in other provinces or during diastems and other breaks. With such independent evidence for reconstructing evolutionary history we are provided a basis for judging whether the close association and the segregations of faunas, floras, genera, and species in systems of rocks have the simple significance that has been assumed. The interdependence of physical and paleontologic stratigraphy and the indefinite role of homotaxis in correlation introduce too much circular reasoning to make it possible to check the capacity of stratigraphic paleontology for proving or disproving the diastrophic theory.

In spite of the vogue of the diastrophic theory, dissatisfaction with its tenets has not gone without expression (Shepherd, 1923). Increasing interest in the lithogeny of sedimentary rocks has led in the last few years to reexaminations of the principles that are implicit in stratigraphic nomenclature. The growth and change of ideas, even in a few years, are well represented in papers by Schenck and Müller (1941), Rastall (1944), Wheeler and Beesley (1948), Hedberg (1948), and Gilluly (1949). Schenck and Müller advocated a clearer distinction between the chronologic and stratigraphic aspects of the historical record. Wheeler and Beesley proposed radical departures from the diastrophic method of dividing the geologic record that are intended to carry to a logical conclusion a recognition of the biologic, lithogenic, and pure time dimensions of the record.

Hedberg's (1948) critical analysis of the "Time-stratigraphic classification of sedimentary rocks" and Gilluly's (1949) direct attack on the uncritical acceptance of the diastrophic theory make it mandatory that the evidence in paleontology for the theory be reexamined.

As one of the purposes of this introductory paper is to describe the meaning of the distribution of evolutionary explosions for geology, many points of overlap and parallel-

ism with Hedberg's and with Gilluly's papers will be found. Their discussion is not only recommended as significant criticism of the diastrophic theory, but as penetrating analyses of reasoning in physical stratigraphy.

In this symposium, the introductory paper will outline the meaning of the subject for geology and will offer an analysis of factors that limit the accuracy of reconstructions of the history of ancient life.

Because the accuracy of geochronology in general and of stratigraphic paleontology in particular are central issues in our discussion and will be the subject of critical analysis, questions and comparisons will naturally arise as to the relative accuracy of this and other methods of geochronology. Mr. John P. Marble, a well-known specialist on age determination by geochemical analysis, will outline the laboratory factors in the accuracy of radiogenic lead methods.

The remaining seven papers will be presented by specialists on important fields in paleontology who will describe the distribution in time and meaning of evolutionary outbursts in the groups of organisms on which they have detailed knowledge.

MEANING OF THE TERM "EXPLOSIVE EVOLUTION"

The term *explosive evolution* or *evolutionary explosion* has sensational qualities, though that is the common term for the phenomenon. Perhaps it was for that reason that Cloud (1948) recently proposed to substitute the term "eruptive," objecting that explosion is commonly defined as a "violent expansion accompanied by a loud noise." Whereas the term explosion is also defined as "a violent outburst of feeling, manifested by excited language," the choice of this term and of this subject for the symposium is a source of apprehension because all of the speakers, with the exception of myself, are likely to make controversial statements. The calmer souls in this audience may have grounds for deciding whether our subject is *explosive* or is quietly *eruptive*.

Explosive evolution has many forms. One form of explosive evolution consists of an adaptation to a condition of living which expresses itself in an extraordinary population. Such an adaptation does not necessarily involve increased morphologic complexity. Adaptive evolution of an explosive type commonly expresses itself in large populations or by accelerated taxonomic diversity and occupation of varied ecologic conditions of living. The extraordinary population of *Endothyra* near the middle of Mississippian time is an example of a population burst without taxonomic diversity. The globigerinids from the middle of the Mesozoic to Recent represent a burst characterized by extraordinary populations with relatively moderate taxonomic diversity.

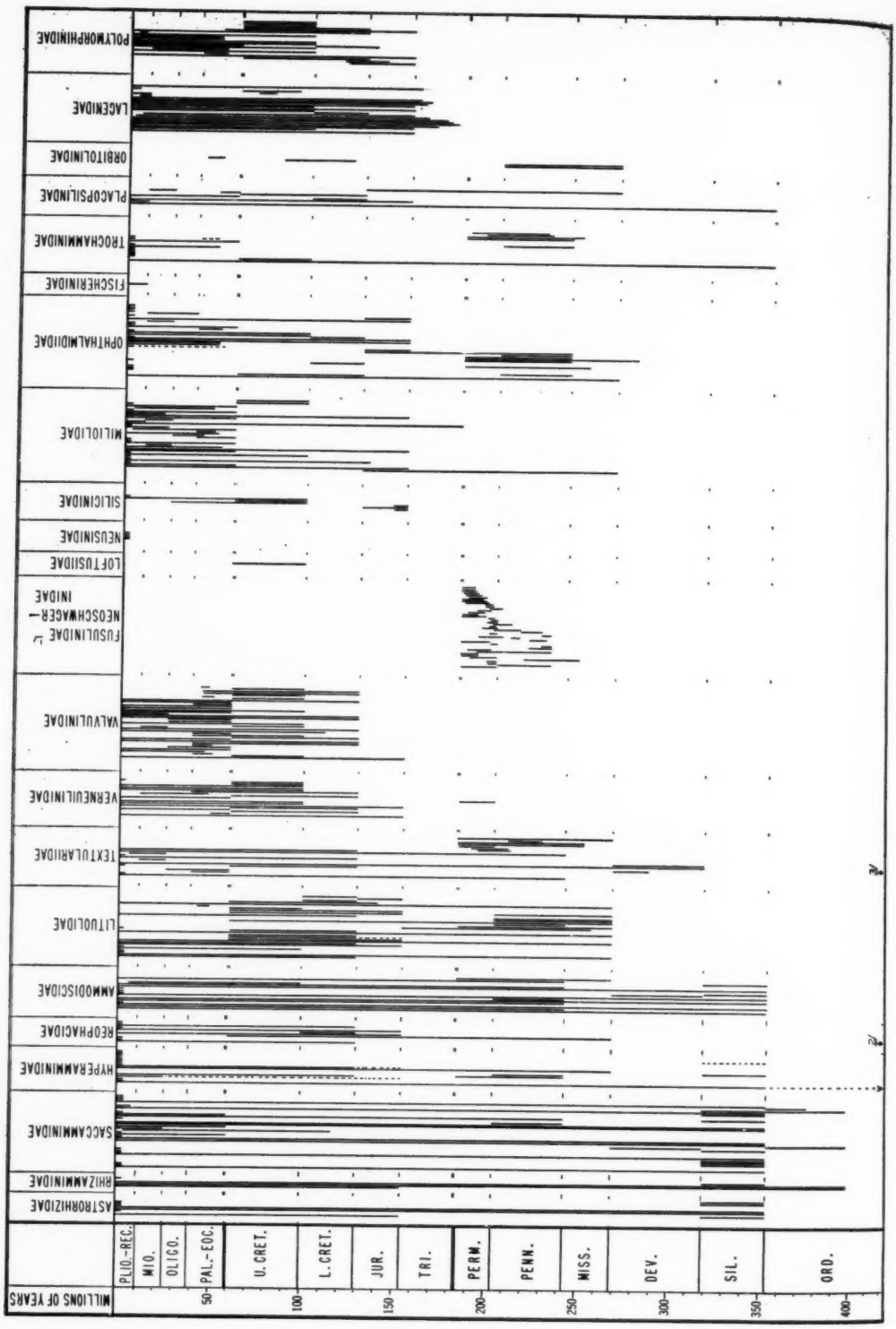
Whether the production of extraordinary populations should be regarded as a form of explosive evolution will depend on whether the increased productivity is the result of adaptation or represents a simple response to exceptionally favorable conditions of living, a distinction that may be impossible to recognize in fossil records.

We are more accustomed, however, to regard explosive evolution as having the properties of increased rate of change, increased complexity or specialization in anatomy, and increased rate of speciation or production of new genera. Among Foraminifera, the Fusulinidae, Nummulitidae, Orbitoididae, and Discocyclinidae are well-known examples. The Fusulinidae rivaled any for morphologic complexity and for great populations and dominance in certain realms of the sea.

Though evolutionary explosions, as the term suggests, are conspicuous features of paleontologic records, their spectacular proportions become modified and less spectacular when the missing parts of paleontologic history are reconstructed. This point will be developed in various connections in this paper and in the papers that follow.

ANALYSIS OF METHODS OF RECONSTRUCTING THE HISTORY OF ANCIENT LIFE

In preparing this paper, a chart was drawn on which the stratigraphic ranges of the genera of Foraminifera were plotted on a geologic time scale. The scale was graduated in millions of years and in geologic periods and epochs. The chart served as a basis for taking census of the genera restricted to periods and epochs, the relative number of genera crossing period and epoch


POLYMORPHINIDAE
LAGENIDAE
ORBITOLINIDAE
PLACOPSILINIDAE
TROCHAMMINIDAE
FISCHERINIDAE
OPHTHALMIDIIDAE
MILIOLIDAE
SILICINIDAE
NEUSINIDAE
LOFTUSIIDAE
FUSULINIDAE
NEOSCHWAGERINIDAE
VALVULINIDAE
VERNEUILINIDAE
TEXTULARIIDAE
LITUOLIDAE
AMMODISCIDAE
REOPHACIDAE
HYPERAMMINIDAE
SACCAMMINIDAE
RHIZAMMINIDAE
ASTRORHIZIDAE
PLIO.-REC.
MIO.
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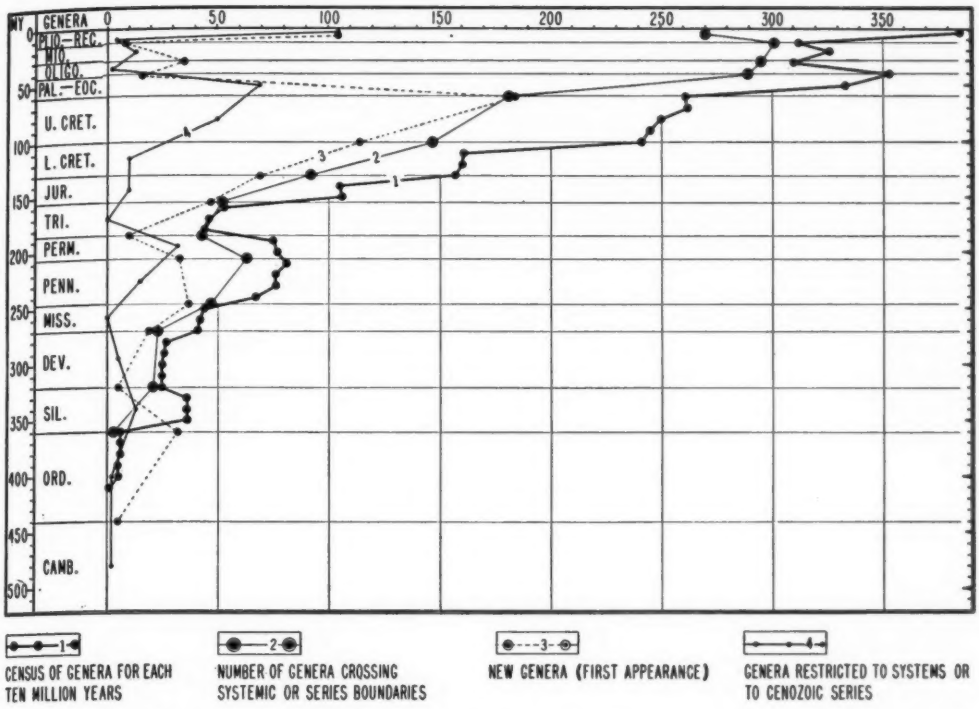

FIG. *2*—Census of foraminiferal genera for each ten million years, number of genera crossing systemic or epoch boundaries, number of first appearances, and number restricted to the geologic systems and epochs of the Cenozoic. This chart represents the order Foraminifera with the exception of the Allogromiidae, which may represent a different class of protozoans.

boundaries, rate of generic proliferation, etc. Half of the chart is reproduced here as figure 1. So many aspects of the methods used in reconstructing the history of the rise and fall of ancient organisms were shown in this simple chart that an analysis of its construction and of its meaning seemed to provide the simplest and clearest way of discussing limits of accuracy in stratigraphic paleontology.

The horizontal grid of the chart, figure 2, consists of lines representing the geologic systems and series of the Cenozoic. The systems and series are spaced according to their durations in terms of radiogenic lead chronology.

The stratigraphic range of each genus of Foraminifera is indicated by a vertical line and the genera are segregated according to families. Cushman's (1948) comprehensive

FIG. *1*—Stratigraphic distribution of the genera of Foraminifera, families 2 to 24 of the Cushman classification. In a few instances where a gap of a period or an epoch intervenes in the vertical range of a well-defined genus, a line for the total range was drawn. It is recognized that this extrapolation to avoid one kind of error may have introduced other errors. (*1*) Fusulinidae and Neoschwagerinidae: The distribution of the penultimate genera in these two families in the latest Permian is not well understood at this time. In the areas of very high Permian rocks so far studied in detail, the environments are not favorable for normal marine assemblages. In Asia, where favorable environments seem to occur high in the Permian, the correlations have not yet been well established. The evolutionary bursts in the suborder Fusulinida show a dendritic pattern and less than average segregation with relation to the systems and series of the time. The family Fusulinidae has been studied in greater detail than most groups of foraminifers and illustrates the principle that the more detailed the record (or sampling) the more the series will display an evolutionary continuum. (*2*), (*3*), Cambrian genus reported.

classification and compilation of the stratigraphic ranges of the Foraminifera were the chief sources of data. Emendations were added wherever necessitated by later or more direct information. Cushman's manual served the purpose well because it is comprehensive and represents not merely a compilation but first hand knowledge of the ranges of most of the genera. An exaggeration of the number of appearances and extinctions at the beginning and end of periods for pre-Cenozoic genera is introduced, however, by Cushman's describing most of the ranges in terms of periods rather than in subdivisions thereof.

The chart displays many examples of evolutionary explosions. In analyzing the logic of its construction, the characteristics of the distribution pattern of genera will be used in some instances to illustrate certain limitations on the accuracy of paleontology and will avoid possible complications on what does or does not constitute an evolutionary explosion.

This graph is not unusual in any way except possibly its detail. It represents a kind of graph that is commonly used in textbooks and syntheses or compilations to give a simple picture of the distribution and of the rise and fall of groups of organisms in geologic time.

Several features of the chart attract attention. First, there are marked segregations of the beginning and of the ending of generic ranges at systemic boundaries and also at series boundaries wherever such are drawn. Corollary with this, marked segregation of the ranges of genera is found within the periods and epochs. This last observation is not affected by Cushman's stating the range of pre-Cenozoic genera in terms of entire periods.

The connection between the distribution of life and the stratigraphic systems of the Northern Hemisphere are striking and obvious. In view of (a) the marked connection shown by the chart between the ranges of genera and to a lesser extent, but still marked, between the ranges of families and the geologic periods or systems and (b) the definition of geologic periods and systems in terms of each other, it is easy to appreciate why the diastrophic theory has seemed to represent a principle of earth history. The problem before us is to determine whether the pattern of distribution shown by the chart represents history accurately or is distorted by integral error.

LIMITING FACTORS IN RECONSTRUCTING THE HISTORY OF ORGANISMS

If the chart and the logic of its making are analyzed, it will be seen that the historic pattern of the graphs is a function of at least 11 variables; namely, (1) Location of the fossil records in relation to centers of culture, research, and mining; (2) natural factors limiting the accessibility of fossil records; (3) factors in the preservation of organisms and fossil-bearing sediments; (4) evolution of facies in a geosyncline and in basins of deposition; (5) method and accuracy of assembling and correlating fossil records; (6) missing records—paleontologic and stratigraphic; (7) exaggeration of the distinctness and of the universality of stratigraphic units by oversimplified age determinations; (8) definition of geologic periods and systems in terms of each other; (9) taxonomic latitude in definition of genera; (10) geographic distribution of organisms; and (11) method of constructing the geologic time scale.

HUMAN GEOGRAPHY AS A FACTOR IN PALEONTOLOGIC DISCOVERY

The location of fossil records in relation to centers of education, research, industry, and mining is an important factor in the discovery and description of faunas. The recent history of micropaleontology illustrates this point. Until 1921 the study of Foraminifera occupied a minor position in paleontology. Under the stimulus of economic use in oil geology the study of Foraminifera rose to a leading position in paleontology within a decade. With some notable exceptions, research since 1910 on series and systems of rocks that figure least in oil geology has lagged the most.

The faunas preserved in systems of rocks that are best exposed in highly civilized communities were among the first to receive study and description. Though disparity of that kind in the quality of our record is being reduced, the human factors alone are largely responsible for the great disparity, for example, in the number of foraminiferal

genera shown in figure 1 for the Pennsylvanian and Mississippian. Intensive research by a single specialist in a period of two or three years on the Devonian Foraminifera and continued neglect of the Mississippian and Silurian would probably reverse the relative curves for those periods. This factor applies in some measure to all stratigraphic paleontology.

EXAGGERATION OF THE DISTINCTNESS AND OF THE UNIVERSALITY OF STRATIGRAPHIC UNITS BY OVERSIMPLIFIED AGE DETERMINATIONS

The geologic history of epochs and periods is never fully represented in the stratigraphic records of a single geologic province. To reconstruct the history of epochs and periods requires the assembling of records from every known province of the world and connecting them in the proper time sequence. This process not only calls into play every known device of age determination and correlation and cross-checks, but involves the handling of enormous quantities of complicated data whose quality runs the entire gamut of conjecture, speculation, and well-reasoned induction. The compiler and the synthesist have no choice but to simplify and sacrifice qualifying details that indicate the quality of the original observations and deductions. This process of simplification tends to pigeonhole the data of historical geology. Data whose accuracy was explicitly or implicitly qualified by the contributor eventually are made to assert a verity they never possessed.

As an example of pigeonholing, the Morrow problem may be cited. The Morrow fauna of Arkansas is transitional and is regarded as containing more Pennsylvanian elements than Mississippian. As our nomenclature does not provide a formal epoch or period name for a unit composed of rocks of Chester and Morrow ages, and such terms as "Mississippian-Pennsylvanian" and "Mississippian and Pennsylvanian" are awkward to use and may be ambiguous, we class the Morrow as Pennsylvanian because it is more Pennsylvanian than Mississippian (there are good authorities who deny even this). With that categorical act we have drawn a line through a succession of Chester and Morrow rocks that actually incorporates certain kinds of evolutionary and sedimentary continuities.

Categorical classification not only afflicts paleontology and geology at the higher levels of synthesis and compilation, it also afflicts every stage of investigation where formations, faunas, and sequences have to be fitted into a rigid system of classification and nomenclature. The process from beginning to end tends to exaggerate the discreteness or distinctness of units within a succession and it exaggerates the degree of contemporaneity with sequences of seemingly similar age in other provinces of the world. It tends to make the records show marked segregation of genera within epochs and periods and marked segregation of the ends of their ranges at the periodic boundaries.

Correlations are commonly made with *the most nearly similar unit in a standard or other sequence.* Such correlations result in exaggeration of similarities and suppression of dissimilarities. This process tends to overemphasize the discreteness of geologic periods and therefore the periodicity of geologic history.

GEOLOGIC FACTORS IN THE ACCESSIBILITY OF STRATIGRAPHIC RECORDS

In earth-structure as in genetics, the present is the child of the past. This truism tends to become obscured because the relationship of existing tectonic patterns and behavior to those of the past are infinitely complex. Nevertheless the tendency of deformations in the earth's crust to follow or to be connected with previous deformations has been widely recognized. The tendency of ocean and continental segments to maintain their general outlines through great lengths of time seems evident though perhaps overemphasized (Ruedemann, 1923; Bucher, 1933, 364–383).

Those trends in the history of deformations give systematic slants and emphases to certain aspects of records of earth history and subdue others. Roughly three-fifths of the surface of the earth is hidden by ocean from detailed examination of historical records. Of the two-fifths remaining, a large share is covered by ice, detritus of glaciation, and tropical jungle. Those and other factors reduce the areas accessible for study

of pre-Pleistocene history to perhaps a fifth or even a smaller fraction of the earth, even though subsurface exploration for oil and new techniques for exploring submarine geology have extended the areas of study.

In stratigraphic columns, even in composite columns of entire geologic provinces, less history is recorded than that not recorded in diastems, unconformities, or other breaks. The principle that the points of observation and areas of exposure of geologic systems decrease toward the past was outlined by Gilluly (1949, p. 576). The position of a system in a geosynclinal succession may also affect directly and indirectly the kind, quality, and relative completeness of its sedimentary and biologic records. A good example is the Pennsylvanian. If we take the records at their face value, the Pennsylvanian was obviously a period of exceptionally lush floras and foraminiferal faunas. The record can not be taken at face value, however, because in no other system of the Paleozoic except possibly the Permian was there a record preserved of such a marked coincidence of broad coastal plain and adjacent shelf seas, climate, and conditions favorable for the preservation of plants as those that characterized this period *in the areas that happen to be preserved and that are accessible to view.*

These factors affect historical analysis by limiting the quality and especially the quantity of sampling of evidence. Inadequate sampling exaggerates the contrast and distinctness between the parts of a gradational series. This applies to the records of an evolutionary continuum whether biologic or stratigraphic.

FACTORS OF PRESERVATION

It is well known that the chances of preservation differ between great extremes among the families, orders, and classes of organisms. Like biologic facies, the sedimentary environments that are favorable for the preservation of organisms are restricted by geologic provinces, tectonic belts, climates, etc., but the conditions favorable for lush growth or taxonomic proliferation may not and often do not coincide with conditions favorable for preservation. A great though systematic disparity generally exists between the original composition of an ancient community of organisms and the composition of the fossil record of that community.

The great scarcity of bird fossils in the late Cenozoic rocks bears little relation to the fauna that probably existed, if we judge by the taxonomic variety and distribution of the existing fauna and project backward the evolutionary trends and rates of change that are deduced from the fossil records that have been found. For North America north of Mexico but including Lower California, 1,420 living species and subspecies of birds were recorded up to 1931. In the same area only 155 species have been found in the Pleistocene. Of these 50 species are extinct and 105 continue into Recent time. The Pleistocene record represents more than half of the fossil species so far found in North America; and as evidence suggests that the bird fauna of late Cenozoic time was richer than that existing today, the disparity between the fossil record and probable richness of the fauna taxonomically is striking. The contrast widens if the number of individuals preserved is compared with the number that probably existed (Wetmore, 1928; Herbert Friedmann, Curator of Birds, U. S. National Museum, personal communication).

Birds possess skeletal and dermal structures that are durable and capable of preservation; but their living habits, predatory enemies, and habitat are such as to preclude burial before the skeletons are destroyed. The chance of globigerinid Foraminifera being preserved in marine sediment is infinitely greater than that of birds in terrestrial sediments.

GEOGRAPHIC DISTRIBUTION

The geographic distribution of the Foraminifera composing evolutionary outbursts would provide significant information on such problems as periodic diastrophism and permanence of continents if it could be reconstructed. Unfortunately, as for most ancient organisms, only a small fraction of the record of ancient geographic distribution is available or accessible for study or has been preserved. This dimension of the distributional pattern is a significant factor in the correlation and dating of events, but can not be reconstructed in detail for the ancient periods.

TAXONOMIC LATITUDE

The taxonomic latitude in the definition of genera and species is a primary dimension of their geographic and stratigraphic distribution. A finely discriminated classification results in increased numbers of genera and species and in corresponding restriction in geographic and stratigraphic range. In a single order of organisms such as the Foraminifera, the value of taxonomic criteria varies from family to family and genus to genus. For example, the specific criteria usable for genus *Fusulina* have no meaning for *Globigerina*. They have dissimilar anatomy. This fact poses difficulties in comparing rates of evolution. With the Foraminifera as with many other microfossils, no person will ever have a chance to see perhaps more than a billionth of the number of individuals of a species. As no two individual specimens are exactly alike, the paleontologist is dealing with an overwhelming complexity of variations. It is a remarkable and deeply significant fact that in spite of inadequate sampling and of complexity, orderly evolution is evident and allows the systematist to predict stages of evolution before they are found. The systematic order that is evident in plants and animals in spite of the fragmentary record is striking testimony of order in nature.

MISSING RECORDS, STRATIGRAPHIC AND PALEONTOLOGIC

Among the outstanding features of the records of ancient life are the abrupt first appearances of many highly developed genera and the breaks in evolutionary lines or "missing links" in other stocks. The subject of "missing links" has been belabored the last 100 years, but its significance as a means of appraising the amount of history not recorded or of records not accessible for study has been neglected.

The family Fusulinidae constitutes one of the most spectacular and one of the more completely studied examples of explosive evolution. An outline of its history is introduced here to illustrate some points apropos to abrupt first appearances and missing links. When *Millerella* first appears, to our knowledge, in the Upper Mississippian, it is a mature form phylogenetically. The earliest forms of the more typical fusiform fusulinids are *Profusulinella* and *Eoschubertella*, which appear in rocks of Atoka age and are more or less intergradational with *Fusulinella*. Intergradations from *Fusulinella* into *Fusulina* and into *Wedekindellina* appear in several species, and high specializations of forms occur at different times in all three genera. *Triticites* first appears in the Missouri group, early upper Pennsylvanian. The record in the European part of the Soviet Empire is not yet quite clear, but in America *Fusulina* ends abruptly in the late Des Moines time and *Triticites* appears in early Missouri time after the most profound break in the history of the family. Judging by the rates and trends of evolution in the forms that are known, *Triticites* should have its ancestral stock among Atoka forms of *Fusulinella* or early Des Moines forms of *Fusulina*. So far the stock leading to this triticite morphology has not been recognized.

In the Central and Rocky Mountain states, the fusulinid stocks comprising the genus *Triticites* expanded rapidly in Missouri time and reached a climax in enormous numbers of individuals and variety of generic proliferation near the beginning of the *Schwagerina* zone in earliest Hueco time. This explosion actually consisted of a succession of accelerating proliferations of stocks that will probably be recognizable eventually as of generic rank. On the basis of the extraordinarily detailed records from these parts of the United States, the proliferations in *Triticites* gained momentum and by the time the stocks became definable as representing *Pseudofusulina*, *Schwagerina*, *Pseudoschwagerina*, *Paraschwagerina*, etc., the evolutionary fission had accelerated into multiple directions simultaneously. Most of the extinctions represent termini of stocks, but many of the extinctions represent only the boundary of taxonomic definition where the fission products of *Triticites* become classifiable as new genera, which might be termed *taxonomic extinction.*

In rocks of Missouri age, ventricosely fusiform species of *Triticites* had their beginning, but the most characteristic stock was the offshoot of cylindrical forms of the group of *Triticites irregularis* (Staff), etc. These reached a climax in the uppermost Missouri time and disappeared from view.

Whether they became extinct after the Missouri time is not known for certain. That the stock may have persisted in some unknown province of the world is suggested by the existence of a morphologically similar form recently found in specimens of rocks of Hueco age, Permian? from West Texas. Whether this represents a relic of the Missourian cylindrical *Triticites* or a new stock is a matter of conjecture at this time.

In Asia, the Upper Pennsylvanian part (i.e., the parts of Missouri and Virgil age) of the *Triticites* zone is missing from the records so far published. As the published records of Asia come from at least 40 or 50 mountain areas and provinces of China, Japan, and other countries, the hiatus seems to be an extensive one and to be continental in breadth. In this country from Kansas to Texas and New Mexico I have seen a number of transitional forms between *Triticites* and *Schwagerina* and *Triticites* and *Pseudoschwagerina*. Though the evolutionary continuum of *Triticites* into *Parafusulina* from the early Missouri division of the Pennsylvanian upward across the Permian boundary is recorded in unusual and perhaps unequaled detail in the central states, there are species in all of those genera that belong to stocks that originated elsewhere. At least their evolutionary stages are not fully represented in the records of the region. Three things about this example of evolutionary explosion need to be emphasized. First, the foraminiferal group has been studied in unusual detail. Second, from the standpoint of geology, the region is one of the more intensively studied areas of the world. And third, as many intermediate stages of development in individual stocks are not recorded, it is evident that much of the evolution that has taken place happened either as more abrupt than usual changes or—more likely—in times not recorded in those records or in other provinces of the world. To experienced paleontologists there is nothing especially unique in the example or in the observations just emphasized. It is recalled here to emphasize the incompleteness of the record and to give evidence for the principle elsewhere discussed that the distinctness of the units comprising an intergradational series (such as historical and evolutionary sequences in geology and paleontology) is inversely proportional to the comprehensiveness of the sampling.

GEOLOGIC TIME-SCALE AS A FACTOR IN PATTERNS OF DISTRIBUTION

If the accepted geologic time-scales are used in reconstructing the distributions of evolutionary outbursts in geologic time, an integral error is introduced in the line of reasoning, because the time-scales and the correlations on which they are based were erected under the influence of the diastrophic theory. If it were possible, an independent time-scale and a more discriminating set of correlations should be employed for testing the theory of periodic diastrophism, but that is not possible for this occasion. The alternative is to use the time-scale which is available and to determine how the scale was constructed in order that we may make allowances for the factors that limit its accuracy.

METHODS OF CONSTRUCTING A GEOLOGIC TIME-SCALE

Of the many ways of constructing and calibrating a geologic time-scale, the principal methods that concern us here are based on (1) evolution of radiogenic isotopes, (2) dating and correlation by fossils, and (3) dating and correlation by physical stratigraphy.

These three methods will be discussed one by one to explore the question whether the dating and correlation of events so far done are sufficiently accurate to decide whether diastrophic events on opposite sides of the earth are synchronous, serial, overlap in time, or fail to conform to a recognizable pattern on a world-wide scale.

In describing the methods of constructing a geologic time-scale it is impossible to avoid overlapping the brief statement of Knopf (1949) on "Time in earth history," which is recommended reading for its clarity and point of view. It is also impossible not to overlap that of Bullard (1945) and especially that of Holmes (1937 & 1947), whose contributions in promoting and synthesizing results of research on determination of time by radiogenic isotopes are so important and well known. Holmes' syntheses, however, have to be read with allowances for the fact that his interpreta-

tions and syntheses are conceived and are fitted into a framework of synchronous, periodic diastrophism, which he seems to accept categorically as a natural law of earth history.

METHOD OF RADIOGENIC ISOTOPES

One of the most notable contributions of this century to historical geology was the discovery of methods of measuring time by radiogenic isotopes. Because results of these methods have an important bearing on the subject of this symposium and its meaning for the diastrophic theory, and because all members of the audience may not be familiar with the actual accuracy of the methods, I have asked J. P. Marble, a well-known leader in this field, to outline the factors of laboratory accuracy.

Before the symposium started, more than one person asked me what connection radiogenic-isotope chronology had with explosive evolution. Having explained here the logical connections, it should be confessed that there were other reasons why we paleontologists invited the enemy into the camp. It was to take his measure and to make invidious comparisons between our methods and his. We can be assured, however, that our competitor will represent his cause with distinction and with an exceptional background of knowledge.

There are at least four kinds of factors that affect the accuracy of the radiogenic-isotope methods. These may be classed as (1) laboratory error, (2) stratigraphic error, or the error involved in dating the source of the radiogenic isotopes in terms of well-established stratigraphic sequences, (3) error from secondary enrichment or depletion of the sample, and (4) analytic error depending on the age of the sample. Mr. Marble will discuss the first, third and fourth factors, and I shall discuss the second.

ACCURACY OF STRATIGRAPHIC CORRELATION OF SOURCES OF RADIOGENIC LEAD

The inaccuracies connected with dating the source mineral of a radiogenic lead specimen in terms of a well-known and a well-dated stratigraphic sequence is a geologic problem. It poses the greatest difficulty that confronts the application of radiogenic-isotope determinations to geochronology. All but a few of the determinations so far made have been based on samples from magmatic bodies and effusions whose relation to well-known stratigraphic successions is obscure except within time limits as broad as entire epochs and periods. The exact time relation of pegmatites to the parent and matrix bodies alone is generally difficult to determine. The exact dating of a sample from the middle of a structural and metamorphic complex, such as that of New England, where the paleontologic data and stratigraphic relations are obscure, or at best vague approximations to a geologic system, speaks for itself. Knopf (1949, p. 5) states that to the date of his writing there were only three "Class I" determinations for which fairly reliable and close stratigraphic connections were known. Those who have only moderate doubts about the diastrophic theory can hardly fail to note that many of the determinations are correlated with standard stratigraphic sequences with conspicuous circular reasoning, which is legitimate, as long as the circular nature of the reasoning is clearly set forth or implied and is not offered as categorical support for a dogma such as that of the world-wide extent of geologic systems and unconformities or hiatuses and "lost intervals."

How was our absolute time-scale constructed? An outstanding and pioneer example of the method was demonstrated about 20 years ago. David White, who was interested in promoting the new method of determining time, interviewed a large number of stratigraphers and stratigraphic paleontologists and asked them to estimate on the basis of rate of organic evolution, thicknesses of sediments, and other such means, the *relative* time values of the geologic systems on which they had worked. The figures that he obtained were averaged. Those in turn were compared with radiogenic-isotope determinations and all were adjusted and fitted together. The figures arrived at separately by stratigraphic paleontology and by isotope analysis agreed more closely than had been anticipated. The results constituted an important event in progress in geochronology. The same

process has been used elsewhere and the sum total of those and related efforts is expressed in such time-scales as those given by Holmes (1937, p. 178) and others. It must be remembered, however, that there are very few isotope age determinations that are not involved in complicated field relations of major proportions chronologically.

Again, I want to emphasize the fact that those efforts marked important advances in geochronology. So far, however, the margin of possible stratigraphic error that must be allowed represents time in terms of geologic epochs and periods. If the margins of error that are described by Mr. Marble are also taken into account, it becomes evident that radiogenic-isotope determinations are insufficient in number and precision to indicate whether the crustal movements of the world are diverse or synchronized and rhythmic.

FACTORS AND LIMITS OF ACCURACY IN STRATIGRAPHIC PALEONTOLOGY

In the discussion that follows I shall go to considerable lengths to point out and emphasize other factors beside those shown in connection with figure *1* that limit accuracy in the methods of stratigraphy and paleontology. For the nonspecialists in paleontology who have not had occasion to weigh the importance of stratigraphic paleontology for geology and who might mistake the intent of these criticisms as destructive rather than constructive, a brief explanation is needed. Knowing the limits of accuracy of measurements, observations, and lines of reasoning is as necessary for wise deduction as knowing the facts—a principle that has been known for at least 2,500 years. The object in the following critique is to describe ways, in addition to those already discussed, in which deductions have exceeded the significance of the data and the accuracy of the measurements. William Smith's discovery of the method of correlating rock formations by comparing their fossils may be regarded as marking the beginning of geology as a science. That method, with numerous refinements since Smith's time, furnished geology with the basic structure of time whereby the connections of events can be diagnosed and cause and effect determined. It was the original method and, with all its faults, remains the most accurate for all but the last brief epoch of earth history; and it is by far the most widely applicable method that we have for correlating geologic records.

HOMOTAXIS

In his "Anniversary address" (1862, p. XLI) Thomas Huxley introduced the term *homotaxis* in order to distinguish between two kinds of correlation. *Homotaxis* as defined by Huxley signified similarity in composition, taxonomy, or position in a sequence without implication of similarity in age. This is distinguished from correlation that will be termed *chronotaxis*, or similarity signifying the same age.

The distinction introduced by Huxley is useful and significant in geochronology, but it has never attracted the attention it deserves, partly perhaps, because Huxley used a badly exaggerated illustration of the principle. The idea of homotaxis is applicable not only to correlation of faunas and floras, but also to the correlation of physical stratigraphic records.

Practically all paleontologic, stratigraphic, and cartographic correlations are homotaxial in some measure. Where chronotaxial correlation is the objective, careful stratigraphers and paleontologists use every means possible to cross-check their correlations to reduce the homotaxial factors to the minimum. Homotaxial correlation may be the objective in delineating stratigraphic and biologic units in transgressive or regressive deposits.

Catastrophic marine invasions, volcanic explosions, and overwhelming invasions of organisms have occurred at times in the past and have undoubtedly left a mark in the records that represent relatively an instant in geologic time. Our ability to recognize such a mark for its true value in time is another question. The criteria for exclusively identifying such events are most generally limited to geologic provinces and rarely or never extend to continental or world-wide breadths. Cosmic catastrophes or cosmic forces such as changes in solar radiation or variations in its transmission through the atmosphere to the earth would affect the climate and life on the earth and leave their marks in rates and kinds of sedi-

mentary deposition. So far such cosmic events can not be clearly and unmistakably recognized as such or as producing responses that can be identified as simultaneous.

Most diastrophic changes are probably long enduring and are complicated by local or general reversals or interruptions. The advances and retreats of the seas and the concomitant transgressions and regressions of marine and terrestrial ecologic zones were generally slow processes. The stratigraphic and paleontologic sequences laid down during one of these advances or retreats may show a detailed and very close homotaxial continuity over a large area but a difference in age in the direction of advance or of retreat may amount to significant fractions of a geologic period. A good example of this is represented by the transgressions of the Rico formation in southwestern Colorado and by that of the Abo and Cutler formations, Pennsylvanian and Permian?, in Colorado and New Mexico (Henbest, 1948).

Dispersal, dispersal by adaptive evolution, and migration of populations take time. These may range from a short time (virtually an instant in earth history) to such a great length of time that the inherent biological factors in evolution may alter the composition of the migrants beyond recognition of their possibly representing a connected series. The paleontologists have certain partial checks on the time element in homotaxis. Forms evolving at explosive rates, free swimming or pelagic forms; plants whose seeds are dispersed by winds, rafts, or animal carriers; and organisms that generate enormous populations and reproduce in enormous numbers may introduce chronologically significant species in fossil communities. The best check for chronotaxis versus homotaxis is obtained wherever vertical sequences of faunas having durations of several epochs are correlated. But the possibility that systems or even larger sequences may possess homotaxial similarity yet be offset chronologically has not been fully explored. The correlation of a single, isolated fauna in a distant part of the world should be regarded with greater doubt than if it occurred in a sequence of related faunas that give opportunity for checks above and below.

The fact remains that it is not possible generally to discriminate accurately to what extent a correlation is homotaxial and to what extent chronotaxial. Each case is a special problem and offers its special opportunity, or lack of it, for cross-check on accuracy. It seems reasonable to expect an accuracy of 9/10 to 2/3 of a Paleozoic or Mesozoic period at most positions in the column in correlations of systems in central and eastern North America and Europe, but between those in the central and eastern part of the United States and South Africa and Asia the inaccuracy may represent a larger fraction of a geologic period. To hypothesize world-wide contemporaneity of orogenic movements or of geologic systems on correlation whose margin of error may equal and in some periods exceed a third of a geologic system, and to assume that the records so correlated and covering but a small fraction of the land areas, actually represent the history of the entire earth will not satisfy most geologists.

ECOLOGICAL ANIMAL GEOGRAPHY AS A FACTOR IN CORRELATION AND CHRONOLOGY

The concept that like faunas or like successions of faunas from widely separated parts of the world represent similar age is based on the assumption that within the great lengths of time with which geologists deal, faunas or floras migrated back and forth over the earth or intermingled and reduced the differences that long periods of isolation would produce. Correlation by general similarity or by similarity of significant elements in the faunas or floras implies that dispersal required but a geological instant. In the early days of stratigraphic paleontology, instant dispersal was generally a fair and valid assumption if allowances are made for the coarse texture of the geological calendar and taxonomy of fossils of the time. Growing knowledge of the factors in ecological animal geography indicates that the early assumptions on distribution did not give adequate weight to factors in distribution and do not satisfy present needs for accuracy.

In spite of recognition of the principle that the present is the key to the past, the meaning of existing ecology and geography

of organisms has not been given the weight it should have in paleontology until the last five or ten years. Anyone who enjoys a sense of well-being over modern accuracy in correlation needs to compare existing marine faunas in recently buried sediment from widely separated shelf-seas in the different ocean basins and estimate for himself how closely he could correlate them.

It may possibly be true, as is commonly assumed, that this is not a fair test because the climate and ecological geography of the present may be a peculiar event in earth history. That this age is especially peculiar remains to be proved and a subject of hypothesis. The differences between the faunas of the Atlantic and the Pacific shelf-seas are definitely not a new event in earth history. The very difficult problem of the correlation of the Oligocene and Miocene of the Austral-East Indian realm with that of Europe and of the Caribbean region might be cited.

The distribution and correlation of the families in the suborder Fusulinida constitute another example. The Fusulinida are divisible into two families, the Fusulinidae and the descendant family Neoschwagerinidae. These families not only produced outstanding examples of evolutionary explosions but displayed different distributions. The Fusulinidae originated at least as early as the Upper Mississippian and first appear in their typical fusulinid form in rocks of Atoka age, basal Middle Pennsylvanian. The Fusulinidae expanded rapidly in population and in specific variety and morphologic complexity and by the middle of Des Moines time became a prominent constituent of the Pennsylvanian faunas of the world and continued to grow in complexity and dominance in its ecologic realm to or nearly to the end of the Permian. The Neoschwagerinidae, evidently an offshoot of the Fusulinidae, developed rapidly in size and complexity of shell structure in the Permian of Asia and parts of the Mediterranean and in parts of the present borderlands of the Pacific. Although the two families are associated in the Asian-Pacific realm, in the central United States where rocks of seemingly similar age and facies are present and where the Fusulinidae are prolific, none of the Neoschwagerinidae have yet been found.

This situation raises the question whether the epoch of the neoschwagerinids is actually later than the marine Permian of the Texas and Rocky Mountain provinces and is absent because no favorable environment existed after the Guadalupe epoch or whether the Atlantic and Pacific realms in which the fusulinids lived were separated by barriers affecting fusulinids during the Permian. The paleontologic evidence so far supports the idea of isolation. If we correlate by the Fusulinidae common to both realms, the zone of Neoschwagerinidae reaches at least as low as the zone of *Parafusulina*, Middle Permian, but some evidence of very uncertain and untested value raises the question whether it may extend back as early as late Hueco time. In addition, though there is much parallelism in the evolution of the Permian genera of Fusulinidae in both the Atlantic and the Asian-Pacific realms, there are also a number of differences, suggesting a lack of free interchange, whose chronological meaning is hard to decide. Peculiarities in the distribution of certain Mississippian metazoan invertebrates indicate that a similar situation existed in Mississippian time.

In the distribution of a marine fauna, for example, it is not sufficient that similar environments exist in different places. Either a favorable avenue or connection for migration must be provided or a means of quick transportation of seed or fertile individuals across barriers must exist. For this reason, the geographic pattern of ecologic realms and the migration or the geographic evolution of those realms in time become as significant in distribution and rate of distribution as the evolution of ecologic facies. Those factors introduce complications in the chronologic meaning of similarity of faunas that are difficult to evalue for exact correlation.

This problem of distribution in time versus distribution in area was strikingly illustrated when Cushman and this writer (1942) were confronted with the need for determining the ages of samples from deep-sea sediments in the North Atlantic. It was found that certain benthonic foraminiferal faunas now living on opposite sides of the North Atlantic differ more from each other than some of the living faunas differ from fossil faunas in the underlying Pleistocene at the same locality.

A deep and seemingly irreconcilable tan-

gle exists between concepts on (1) permanence of ocean basins, (2) rates and kinds of diastrophic changes, (3) land bridges, (4) rates of dispersal, and (5) phylogenetic relations and geographic distribution of groups of organisms. To speak confidently of faunal and floral diffusion as occupying but an *instant* of geologic time is to ignore the meaning of these enigmas for the resolving power of stratigraphic paleontology.

RATE OF EVOLUTION AND OF RADIATION AS A LIMITING FACTOR IN CORRELATION

The radiation of organisms depends on biologic factors as well as on the changes of environment induced by diastrophism. Adaptation, changes in population pressures or competition, and other aspects of evolution are superposed on the rates of migration of environments produced by diastrophism. Dispersal by natural or accidental means of transportation or rafting across ecologic barriers may effect an instantaneous distribution from a geologic standpoint. The distribution of all organisms is controlled by the distribution of the food they prefer or are willing to eat. Organisms capable otherwise of broad ecologic and geographic range may occupy only a fraction of the realm because the organisms on which they depend for food are restricted to a small realm. Under some conditions, however, a new source of food may induce organisms to adapt themselves to a new environment or a new province.

The preceding factors introduce variables and unknown quantities in correlation. With demands for increasing precision they can no longer be ignored as limitations.

One of the striking features of figures *1* and *2* is the acceleration of the evolution of new forms. Such acceleration is evident at ordinal, family, and generic levels in the Foraminifera. Figure *2* gives the curve of acceleration for the order. The interpretation of the graph needs, however, to be modified not only by the factors that have already been discussed, but by the following considerations:

1. The potential of taxonomic discrimination increases as the morphologic complexity of the organism increases. In other words the more recent and highly specialized organisms tend to have more kinds of features by which the taxonomist may recognize change and taxonomic division than do the more generalized forms.

2. Variety and representativeness of sampling increases upward because (a) In general there is progressively less metamorphism and destruction of fossils in recent than in ancient rocks, and (b) In general, larger and more numerous areas of recent than ancient rocks are preserved, exposed, and accessible for study (Gilluly, 1949).

3. Resemblance and genetic kinship with existing forms of life become closer toward the Recent. This increases the areas of understanding and makes finer taxonomic divisions possible.

Certain important exceptions to all of these factors can be demonstrated but the factors apply by and large. These factors apply to our problem in two ways. They not only modify the concept of acceleration but they indicate why correlations by stratigraphic paleontology should increase in detail and in accuracy as the Recent is approached. This trend in potential of accuracy could and may actually be counteracted to some extent by intensifying division of the earth into climatic and geomorphic provinces, if such intensified division has actually occurred.

The preceding factors do not necessarily deny that there is an accelerating tempo in evolution but they do show that appearances may exaggerate the facts. The rate of evolution is in many respects a relative matter. The rate of evolution in the lowly *Amoeba* is difficult to estimate because most of its morphologic and its physiologic complexities are immeasurable by existing techniques. In the evolution of complex organisms, changes are more perceptible.

The possibility exists of course that the increasing tempo in generic production of organisms in general may be a feature of cosmic evolution. Milne's hypothesis of "kinetic acceleration" is an interesting speculation along this line, but the difficulty with proving this hypothesis is that the forces that increased the rate of physical and organic changes may have similarly increased the rate of the flow of time or at least the speed of the clocks by which we measure time.

A factor of unknown value in correlation is the probability that faunas and floras

that become divided and isolated may and perhaps often do evolve in the same directions but at different rates before one or the other undergoes changes that serve to distinguish them.

FACTORS LIMITING THE RANGE AND ACCURACY OF CORRELATION BY PHYSICAL STRATIGRAPHY

The breadth of significance of physical stratigraphy for geochronology is largely provincial. The local successions of sediments have furnished the starting point whereby faunal and floral successions are established by the law of superposition. Such reconstructions usually represent an integration of paleontology and stratigraphy. A great difference of opinion, not to say confusion, exists over the geographic and chronologic continuity of formations, series, systems, and unconformities. The difference of opinion ranges all the way from regarding the continuity of those divisions as restricted to provinces to regarding it as world-wide and even bearing the marks of cosmic rhythms.

Regarding the world-wide continuity of physical stratigraphic features in a system of rocks as a means of correlation, suppose the sediments of the present day had been subjected to all of the manifold events that were imposed on a Paleozoic system. How would one recognize any physical clue as to contemporaneity of the polar tillites, East Indian volcanics, tropical carbonates, or Gulf Coast muds? It isn't sufficient that we recognize contemporaneity between New Jersey and Florida shelves or between the faunas of opposites sides of the Atlantic. On the scale and accuracy assumed or implied in the diastrophic theory, correlation to fractions of a period as small as or smaller than geologic epochs on opposite sides of the earth is required.

So far as can be determined, there is no clear or unmistakable imprint of a cosmic force in the stratigraphic record of any epoch. Whether variations in solar radiation at the source or as a result of complications in the orbits of the planets, or whether a series of enormous volcanic explosions have changed the weather and consequently the rates of erosion, inaugurated ice ages or the evolution of life are matters of speculative hypothesis. *At any rate, with the exception of atomic evolution of certain elements, there is no known, single physical feature that exclusively characterizes and serves to identify the rocks of any geologic system or series on a world-wide scale.* In general, Cambrian rocks are more lithified than Silurian, and Cretaceous are more lithified than Pleistocene. More redbeds are found in the Permian and lower Mesozoic rocks than in the Devonian and Mississippian rocks of North America. Bituminous coal is especially characteristic of the Pennsylvanian of North America and Europe. But age determinations on such physical criteria could err as much as a geologic period or epoch in a strange geologic province.

SIGNIFICANCE OF UNCOMFORMITIES

The significance of unconformities is a question of rather curious position in stratigraphy and historical geology. Unconformities are one of the most common and significant features of stratigraphic records, yet they are often more difficult to interpret than the formations they separate. Generally the significance of an unconformity can not be appreciated until an analysis of the events attending its origin can be made throughout the province of its distribution. There are few features of a stratigraphic record about which more easy and more confused generalizations have been made.

T. C. Chamberlain in his presentation of the theory of "Diastrophism as the ultimate basis of correlation" (1909, p. 691) indicated that the value of an unconformity varies from place to place. Chamberlain and Salisbury (1906) stated that " . . . all unconformities are presumably limited in extent." These authors and Blackwelder (1909) present significant information on the transgressive and provincial nature of many broad unconformities. In spite of these and similar analyses, the concept of catastrophic "world-wide" breaks dies a hard death. Simple reflection on the nature of the degradation of land areas and silting of basins should indicate that a "world-wide break" or a "world-wide unconformity" is a physical impossibility by any process so far known to have operated on the earth. Erosion is always accompanied by deposition. So far we have no proof that all of the sediment of any epoch or interval is permanently lost

to the seas. Every unconformity must *originally* have interfingered or changed laterally in some direction into sedimentary sequences that recorded the events in the hiatus of the unconformity. Waves of an advancing sea, planing off the land as it advances, will wash and grind the detritus and lay it down to the rear. Though the new rock formation formed by this detritus must be younger than the unconformity it overlies in any one place, it will necessarily be older than the extension in time-space of the same unconformity remaining to be formed by the same advancing sea. Some marine invasions may have been abrupt or cataclysmic and the consequent break in sedimentation may have represented synchroneity over the basin invaded. I believe, however, that the majority of geologists regard the evidence as overwhelming that marine transgressions and regressions were generally progressive rather than cataclysmic. To recognize the progressive, evolutionary nature of marine transgressions and regressions and at the same time to use unconformities or hiatuses as unqualifiedly synchronous datum planes represents a confusion of elemental proportions. Furthermore, the generalization that important transgressions and regressions represent but instants of geologic time constitutes, from evidence I have seen, a gross oversimplification.

It is widely observed that orogenic movements express themselves in a complex of ways. The uplifts of a single mountain range may expose land on one side and form a basin that receives and preserves a sedimentary record on the other. The rise of whole mountain systems may be and perhaps commonly are accompanied by local reversals or variations of movement as to (1) the direction, (2) the time of initiation, and (3) the rate of progression or duration. A detailed and precise chronologic analysis of the record of an orogenic movement by all the techniques at our command becomes incapable of resolving the exact points of beginning or of ending.

DISSIMILARITY BETWEEN THE STRATIGRAPHIC RECORDS OF DIFFERENT CONTINENTS

The striking dissimilarities between several important stratigraphic sequences in the Northern and Southern Hemispheres have not received the attention they deserve. In synthesis in historical geology there has been a tendency to search for and dwell on points of similarity in the columns under consideration with the European type sections. The points of dissimilarity get less attention.

One of the most conspicuous examples of dissimilarity is in the rocks of Karoo (Gondwana) age of Africa. The Karoo problem has been outlined in the "Report of the Commission on the distribution of the Karoo (Gondwana) system," which commission was created by the Fifteenth International Geological Congress and was composed of the directors of eighteen geological surveys in Africa, Eurasia, and South America and a few individual geologists (Haughton et al., 1936).

Du Toit (1939, p. 11) gives a more detailed account of the problem in South Africa. He states that " . . . it unfortunately happens that few of the great evolutionary cycles were absolutely universal, in consequence of which it is found that the 'diastrophic' periods in South Africa do certainly *not coincide* with those in Europe. Nearly every important break in South Africa, paleontological as well as stratigraphical, happens to fall somewhere within one of the European Systems, and each more or less well-marked unconformity between the Systems in the Northern Hemisphere is usually represented in this country by continuous deposition. . . . "

In South Africa, the rocks of Silurian, Devonian, and a part of the Mississippian age comprise a 10,000-foot succession of sediments that are called the Cape system. That is followed by the Karoo system, about 20,000 feet thick, which straddles the Paleozoic-Mesozoic boundary and comprises a lithogenic entity extending from and including a part of the Mississippian up to and including a part of the rocks of Jurassic age. The Karoo system is followed above by the so-called Cretaceous systemic unit which includes the upper part of the rocks of Jurassic age in addition to those of early and late Cretaceous age (Du Toit, 1939; Haughton et al., 1936, Haughton, 1938).

Wadia (1919, p. 36) states that "An outstanding difficulty in the study of the geology of India, is the difficulty of correlating

accurately the various Indian systems and series of rocks with the different divisions of the European stratigraphical scale which is accepted as the standard for the world." Wadia continues (pp. 36–37) to point out that such similarities as exist biologically and lithologically between the European and Indian sections should not be regarded as indications of absolute contemporaneity between the divisions in such distantly situated provinces. Wadia (pp. 44–46) groups the Cambrian to Pennsylvanian (inclusive, except possibly Upper Pennsylvanian) together as the Dravidian "group." The "Permo-Carboniferous" and Permian to Jurassic inclusive are assembled as the Gondwana system of the Aryan "group."

Returning to the correlation of the Cape system, the existence of the Devonian fauna in the Cape system, which is said to have a remarkable similarity to certain Oriskany faunas in New York and South America, does not contradict the emphasis above on the dissimilarities reported to exist between the columns in the Southern and in the Northern Hemispheres. The same writers who have commented on the similarity between the South African fauna and the faunas of the Oriskany of New York also commented on the absence of a similar fauna in Europe. Without stressing the doubt I have heard expressed, that the South African fauna is actually as closely similar to the fauna of the Oriskany as was thought, the points of world-wide similarity involved here as evidence for synchronous diastrophism leave much to be desired. Again, it appears that emphasis on similarities and inattention to dissimilarities—an inadvertent selection of evidence—have been practised.

In the face of such discrepancies it might be argued, of course, that more detailed work would disclose an order in the stratigraphic successions in the Southern Hemisphere that corresponds to the classic successions in Europe and the United States. Such a possibility must be entertained but the conjecture does not appear to have much weight in view of the array and competence of the geologists—trained in the European tradition—who have wrestled with this southern problem. It seems to be a fact that the differences of distribution in time between breaks, unconformities, and lithogenic units of the northern and southern halves of the world are more conspicuous than the similarities. This is devastating for the notion that geologic systems are synchronous, world-wide divisions of the stratigraphic column and represent world-wide rhythm of crustal movement.

CLASSIFICATION AND NOMENCLATURE OF STRATIGRAPHIC UNITS

The influence of the diastrophic theory is more clearly shown in the stratigraphic classification of rocks than perhaps in any other area of geologic reasoning. Critical aspects of the philosophy implicit in stratigraphic nomenclature have been treated by Schenck and Muller (1941), Rastall (1944), Wheeler and Beesley (1948), and Hedberg (1948). Whether the concept of the so-called time-rock unit that is gaining favor promotes clarity or confusion of thinking remains to be seen, but the emphasis on clear distinction between the dimensions of time and of lithogenic units represents progress. Though Hedberg has covered the field with a penetrating analysis, I wish to add a few notes apropos of the fundamental, world-wide divisions of the historic record, periods and systems.

In the American Code of the "Classification and nomenclature of rock units" (Ashley et al., 1933), Article 2 (1) defines the geologic system as "a standard, world-wide division; contains the rocks formed during the fundamental chronologic unit, a period. (See Article 24.)" Article 24 (2) states that the geologic "Period [is] the fundamental unit of the geologic time scale, the time during which a standard system of rocks was formed. . . ." These units are defined in terms of each other. The circularity here is acceptable under the diastrophic theory, and perhaps to most it offers no special problem. To those who have dealt with correlation on a continent-wide or world-wide scale, the circularity represents an enigma that has plagued their efforts at integrating and classifying stratigraphic records.

This enigma was recognized by those who drafted the code (J. B. Reeside Jr., personal communication). The definitions give room for a more objective and less theory-bound practice by delimiting geologic periods by the duration of a "standard system of rocks"

and by allowing such additions of units from other provinces as may be needed to complete a world-wide time division. This gives some room, at least, for recognizing and classifying systems, series, and formations on the basis of their lithogenic, homotaxial, and transgressive properties, provided that it is clearly indicated that these divisions do not necessarily represent time levels or correlate exactly with the time of the standard column.

The employment of a dual system of classifying the geologic record encounters two kinds of difficulty. Evolutionary bursts and periods in each major realm of life tend to occur in tandem sequences. The waxing of one group is likely to be complemented by the waning of another or vice-versa. As a consequence, the periods and epochs of the phyla, classes, and orders of plants and animals do not approach coincidence closely enough to allow the substitution of biologic periods for geologic periods. For the same reason, faunal and floral zones are not satisfactory substitutes for time or lithogenic zones. If we add to that complication the limitations that result from the fragmentary character of the paleontologic record, the difficulty of recognizing time zones by fossils can be appreciated. The biologic diastems within systems and series of fossil-bearing rocks and the biologic dark ages in the intervals between the systems and series of rocks may confuse or mask the record of biologic periods and epochs.

Though the stratigraphic paleontologist has various partial checks and cross-checks that can generally be applied in correlation, many situations are encountered where the natural lithogenic divisions represent the closest approximations to time divisions that are feasible in any one locality

SUMMARY AND CONCLUSIONS

In the previous discussion of the limiting factors in the accuracy of stratigraphic paleontology and in physical stratigraphy, I have made an effort to point out every possible kind of logical limitation and have not made equal effort to balance that with "constructive criticism." Such effort seems "destructive" and derogatory to some. Such, however, is far from my motives. I firmly believe that one of the chief sources of the preeminent strength in the scientific method of reasoning is its predilection and capacity for finding fault with itself. I regard the discovery of a fallacy as an act of constructive criticism.

Temporary damage can be done, however, if anyone gets the mistaken idea that the value and accuracy of stratigraphic paleontology have deteriorated. The significance of geophysical and sedimentologic methods of correlation remains local or provincial in scope. The methods of age determination by radiogenic isotopes have world-wide application but so far have but a fraction of the applicability of stratigraphic paleontology and have furnished so far only a few dates of first-order stratigraphic significances in the Paleozoic, Mesozoic, and early Cenozoic. But this field of science is in its infancy. The intensified interest in paleoecology and in the micropaleontology of Foraminifera, diatoms, spores and pollen, and many other fossils has widened the scope of nonvertebrate paleontology to include terrestrial as well as marine sediments and to increase the accuracy and geological significance of its discoveries. The use of stratigraphic paleontology in furnishing the warp and woof of historical geology has increased phenomenally and has not nearly exhausted the resources of the present methods. Generalizations such as the diastrophic theory represent dogmas that have outrun the verifiable meaning of their basic data. The diastrophic theory may prove to represent an integral characteristic of earth history, but the evidence is insufficient to prove that such is true.

The evidence from stratigraphic paleontology as it appears to this writer indicates that the diastrophic theory and some of its corollaries that are applied in stratigraphy represent greatly oversimplified and exaggerated inference. It is also this author's view that, as we progress in filling gaps in stratigraphic records and reconstructing the history of the earth, the lines of evolution will emerge as paramount and the gigantic synchronous pulses will become more diffused and obscure as integral properties of earth process.

Criticism of contemporary emphasis on diastrophic rhythm needs to go further than to call attention to theory having outrun fact. Not only has evidence been so exaggerated or uncritically used as to prejudice

the thinking of the student, but the character of earth history is distorted by classifying events to fit into a mold. Such a trend can have no other effect than that of obscuring or belittling the evolutionary character of earth history.

One of the most characteristic features of the present epoch of historical analysis in geology is the extension of the principle of rhythmic succession into every aspect of geologic process. Without intending to deny that rhythm or vibration is a common characteristic of natural processes, it is evident that the theorizing on rhythm in nature has outrun the facts and possibly its actual importance. The dramatic appeal of "The pulse of the earth" (Umbgrove, 1947) is stimulating and captures the imagination. It recalls the Greek tragedy whose essence was not unhappiness but the "solemnity of the remorseless working of things" (Whitehead, 1925, p. 11). In spite of the persuasion of such depictions of diastrophic rhythm as that of Holmes (1937) and of Umbgrove (1947), to mention but two of the most admirable, we must dig beneath appearances to see how the data are reasoned.

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Many of the ideas that are offered in this paper have been discussed in years past with Dr. J. B. Reeside, Jr., of the U. S. Geological Survey. These discussions have been a source of stimulation and have clarified points of view, for which I wish to express the warmest appreciation.

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SOME OBSERVATIONS ON THE ACCURACY OF THE "LEAD METHOD" FOR THE MEASUREMENT OF GEOLOGIC TIME

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ABSTRACT—The "lead method," involving the determination of the ratio of Pb to U+Th by chemical analysis, and its correction for "common" Pb content by measurement of ratios of the Pb isotopes is the most widely used method for the absolute measurement of geologic ages. The method is based upon: (1) the constants of radioactive decay; (2) their constancy throughout geologic history; (3) chemical analysis of a suitable mineral for Pb, Th, U; (4) separation of the contained Pb, free from interfering elements, in a form suitable for the accurate measurement of the ratios of its isotopes; (5) measurement of these ratios; (6) and, very important, adequate laboratory and field study of the mineral used, to determine presence of leaching, enrichment, and the like. Present methods for the study of these points, and of their accuracy, will be discussed.

INTRODUCTION

THIS brief discussion contains no new data, but since the material on which it is based is scattered through the literature of three sciences, and since some of it is phrased in terms that, perhaps, are not familiar to paleontologists, it was thought to be worth while to present a very condensed account for this occasion. As suggested by Dr. Henbest, what follows is concerned only with the laboratory studies involved, plus a few words as to the fundamental constants upon which such studies are based. The relation of a radioactive mineral to its host rock, the relation of its immediate host, e.g. pegmatite or hydrothermal vein to the main igneous body, and the relation of the igneous body to the fossiliferous sedimentary rocks of the neighborhood (oft times far distant) are problems beyond the ability of a simple analytical chemist to discuss. Suffice it to say that there are probably more interesting and unsolved problems in these fields than in the physical chemistry involved in what follows.

It must be made clear at the start that a thorough "lead age" determination is not a simple individual physical measurement to which a mathematically computed probable error of $\pm x$ million years can be assigned. It is an extremely complex qauntity. The errors involved in each part differ widely. Some errors are a function of mineral composition, some of relative age, some of the proportion of the chemical elements involved in the computation, and some of the "constants" in the equations used. Thus each "age determination" must stand on its own feet. Furthermore it must be borne in mind that we have to use the material with which the Almighty provides us, and this material is never ideal and seldom suitable. It should hardly be necessary to mention this to a geological audience, but the writer has observed a certain naïve reliance placed by some geologists on the results of other sciences applied to geologic material, and at times the drawing of conclusions therefrom that the physicist or chemist considers unwarranted.

To state the problem in a very simple form, a *complete* "lead age" measurement, using existing techniques, requires or is premised on the following:

(1) The fundamental constants of radioactive decay.

(2) Knowledge as to the invariability of these constants throughout geologic history.

(3) A chemical analysis of the particular mineral for uranium, thorium, and lead.

(4) The conversion of a sample of the lead into a suitable form for the determinations of the ratios of its isotopes.

(5) The measurement of these isotope ratios.

(6) Field and laboratory studies as to the "freshness" and other aspects of suitability of the mineral for use as an "age index."

The order in which these topics are arranged is that of their fundamental historical development, and is considerably different from the procedure to be followed when a new mineral sample is reported. Let us consider each of these points in the order given.

FUNDAMENTAL CONSTANTS OF RADIOACTIVE DECAY

Each of the elements in the three natural radioactive series has its own half-life, i.e. that time by which one-half of the element originally present (or formed from its immediate parent) has decayed to the next element in the series. Since the half-lives of the three parent elements are by far the longest ($T_{UI}=4.56\times10^{9}$ yr.; $T_{AcU}=7.13\times10^{8}$ yr.; $T_{Th}=1.389\times10^{10}$ yr.) (1), when radioactive equilibrium has been established, i.e. when each daughter element is decaying as fast as it is formed, which takes c. 1 million years, these constants are the governing ones in the formation of the stable end-products, the lead isotopes Pb^{206}, Pb^{207} Pb^{208}. For a discussion of the rôle of these changes, see, below under 5. The half-lives of each of the parent elements are known to within about 1 part in 1,000, so that the error is much less than for any other values involved. Any changes found by research still to be done will have virtually no effect on minerals of Paleozoic or younger age, and will only change ages in the Precambrian by, say, 1 to 5 million years in ages of from 600 to 2,000 million years—which will be negligible. It might be stated that the values for T_{AcU} and T_{Th} are probably slightly less accurately known than that for T_{UI}. The effect of lack of or interruption of radioactive equilibrium will be considered briefly below under 6. The value of the ratio T_{U+AcU}/T_{Th} is not quite as accurately known. The value lies between 0.333 and 0.36, varying with age as a second order effect. This ratio is the "k" in the so-called "approximate age ratio," Pb/U+k Th, and hence of some importance. Research now in progress is expected to clear up the present uncertainties.

INVARIABILITY OF CONSTANTS OF RADIOACTIVE DECAY

There is a considerable body of astrophysical evidence scattered through the literature which indicates that nowhere in the known sidereal universe is there any source of natural energy sufficiently great to alter a rate of natural radioactive decay once the process has started. The recent development of artificial sources of extremely high energy has not revealed to date any published data to show that bombardment affects these natural rates. True, a new type of decay can be caused by bombardment, but the remainder of the bombarded material appears to continue to decay normally after removal of the artificial energy source. In any event, such high energy particles do not exist in nature.

It has been shown by Seaborg and his colleagues that the cosmic ray neutron should cause fission of the uranium nucleus in the field, but search by them for the amount of plutonium and other transuranium elements (2) indicates, by negative evidence, a maximum of 1 part in 10^{14} of such elements in several minerals. Also the various studies on the half-life of "natural fission" caused by the bombardment of the uranium or thorium nucleus by its own occasionally high energy alpha-particles indicate this to have the value of about 10^{16}–10^{17} yr. (3), which again is entirely negligible as compared with the normal decay half-lives of 10^{9}–10^{10} yr.

The most positive evidence for the constancy of the natural decay rates is found in the work of the late G. H. Henderson (4), who studied the radii of pleochroic haloes in mica by a most precise method. These haloes are caused by the bombardment of the mica by alpha-particles from the radioactive nucleus. Henderson found that the ranges of the particles, and hence their energy, and consequently their half-lives, were the same in micas of varying geologic ages, and that when the range in mica was converted to its equivalent in air, the values were identical, to within 1 part in 1,000 with those found today in the laboratory. It thus appears that no change in radioactive decay rates has occurred at any time in the known geologic past.

CHEMICAL ANALYSIS FOR URANIUM, THORIUM, AND LEAD

Our troubles begin with analysis of a mineral for uranium, thorium, and lead. All radioactive minerals are of extremely

complex chemical composition. This means that a great many steps are necessary in order to separate the uranium, thorium, and lead in a pure form, and consequently that the accurate quantitative determination of these elements is difficult. Further, a number of different types of minerals are involved, so that different methods of attack are required, as well as very varied analytical schemes. Still further, uranium is often only a minor constituent, thorium nearly always so, and lead always such. Thus the errors inherent in all analytical procedures pile up on the essential elements. As the age depends in the first instance upon the ratio Pb/U+Th, any error in the determination of lead has an enhanced effect, since errors in the numerator of a small fraction are more important than errors in the denominator.

It is essential, therefore, to take particular pains in age analyses, not only as to operations and choices of methods, but especially as to purity of reagents. Acids and ammonia should always be carefully redistilled and solid reagents recrystallized to ensure complete freedom from lead. When the lead has been separated from the uranium and thorium, such precautions are not as essential in the determination of the two latter elements, since all analytical reagents contain a few parts per million of lead, but are free from all analytically significant amounts of uranium and thorium. The procedure of adding a lead precipitant to the reagent and filtering is not thoroughly reliable, as the conditions are not always those that permit a quantitative precipitation of lead.

It should be obvious that an age analysis is not a job to hand to a novice analyst, but requires the judgment that comes with experience. Under 6 are noted some points which suggest that the analyst should have had mineralogical as well as chemical experience.

In spite of all these gloomy statements it is possible to get good analyses made. Below are listed a few instances, showing either agreement between duplicate analyses of the same sample, or between analyses of different samples from the same source.

In general it may be said that with due care, the determination of lead and uranium can be carried out with the expectation of

I. "Pitchblende," Great Bear Lake, Northwest Territories, Canada (5)

No.	%Pb	%Th	%U	Pb.U +0.36Th
2	—	[0.009]	52.405	—
3	—	—	52.209	—
5	10.502	<0.005	52.133	0.2014
6	10.462	<0.005	—	—
7	10.509	<0.005	52.203	0.2013
8	10.480	<0.005	—	—
12	10.529	[0.008]	52.414	0.2009
13	10.559	—	52.534	0.2011
14	—	0.004	—	—
Ave.	10.507	0.004	52.316	0.2012

$$\frac{10.507}{52.316+0.36\times0.004}=0.2008$$

(Duplicate analyses made on one sample)

II. Allanite, Whiteface Mountain, Essex County, New York (6)

No.	%Pb	%Th	%U	Pb.U +0.36Th
1	—	1.045	0.077	—
2	—	1.064	0.060	—
4	0.079	1.074 1.068	0.062 0.062	0.176
5	0.072	1.073	0.079	0.154
6	0.076	1.092	0.074	0.163
Ave.	0.076	1.079	0.069	0.164

$$\frac{0.076}{0.069+0.36\times1.069}=0.167$$

(Duplicate analyses made on one sample)

III. Uraninites from Pegmatites of Northeastern Karelia, U.S.S.R. (7)

No.	%Pb	%Th	%U	Pb.U +Th[1]
1	18.10	0.13	61.14	0.295
2	18.78	0.01	63.71	0.295
3	19.01	0.01	62.61	0.304
4	19.09	0.01	63.08	0.303
5	19.12	0.01	63.05	0.303
6	18.88	—	62.73	0.301
7	18.10	0.60	62.82	0.285
Ave.	18.73	0.11	62.73	0.298

$$\frac{18.73}{62.73+0.11}=0.298$$

(Analyses of various samples made by several anlysts)

[1] Note that this is not Pb.U+0.36Th, as before. A different method of age calculation was used in this work.

good agreement between duplicate analyses, but thorium may be expected to show a greater proportionate variation, especially under certain conditions of thorium content and of chemical combination, which are not yet fully clear. An unpublished example of a preliminary series of analyses by the writer brings this out.

IV. URANINITE, BOQUEIRÃO, RIO GRANDE DO NORTE, BRAZIL

No.	%Pb	%Th	%U	Pb.U +0.36Th
1	5.09	0.60	75.79	0.067
2	5.12	0.29	75.78	0.068
3	5.08	0.17	75.76	0.067
Ave.	5.10	0.35	75.77	0.067

In this instance the percentage of thorium is small and has very little effect on the value of the ratio, but such is not always the case. The difficulty perhaps lies in the methods for the determination of thorium, which all depend on its separation from the usually much larger amount of rare earths by repeated fractionation, a process which is never highly quantitative. It is to be hoped that forthcoming declassification may reveal better methods.

CONVERSION OF SAMPLE FOR DETERMINATION OF RATIOS OF LEAD ISOTOPES

Unfortunately the determination of the lead ratio is not the final step in the computation of an absolute age. Lead has a very dubious distinction among all the chemical elements, in that there is more than one kind of lead. Leaving out of consideration for the moment the individual isotopes of this element, there are essentially two varieties of lead:

A. Common lead, i.e. the lead found in the sulfides, arsenides, etc., and in their oxidation and weathering products. This is an ordinary stable element, formed by the same processes as other similar elements, but what these processes are is at present unknown.

B. Radiogenic lead, i.e. the lead which is the stable end-product of the radioactive decay of uranium and thorium, and is formed only as the result of this type of decay.

Since uranium- and thorium-bearing minerals are sometimes found in vein deposits carrying sulfides, etc., and since the pegmatites, which are a favorite habitat of radioactive minerals, occasionally carry minor amounts of sulfides, there is the ever-present possibility that not all of the lead found by chemical analysis is radiogenic and hence that the lead ratio is not a true measure of the absolute age of the mineral. It is obvious that, in the absence of the removal of lead by leaching or other processes, the lead ratio uncorrected for the presence of common lead gives us a maximum value for the absolute age, but we cannot tell how much less than this the correct age is without carrying through two more steps.

It has been shown that the chemical atomic weight of common lead has the average value of 207.21. The chemical atomic weight of radiogenic lead varies between the upper limit of about 208.0 and the lower limit of about 206.0, depending upon the relative proportions of uranium and thorium in the mineral from which it is extracted. The "common" lead contamination in a mineral containing such proportions of uranium and thorium as to yield a lead of atomic weight of 207.2 would be virtually impossible to compute, although efforts to do so have been made. For minerals containing virtually no thorium or virtually no uranium, the correction can be made with relative ease and considerable accuracy, but a chemical atomic weight determination requires several grams of purest lead salt and several months to carry out.

The introduction of the concept of the isotopic composition of all elements and the development of the methods of accurate quantitative mass-spectroscopy for measuring the isotope ratios of the elements, largely by A. O. Nier (8) has shown that the following are the relationships involved:

UI (U^{238}) decays to Pb^{206}
AcU (U^{235}) decays to Pb^{207}
Th (Th^{232}) decays to Pb^{208}.

Thus a "pure radiogenic" lead will contain a proportion of these *three* isotopes depending upon the proportion of the "mother elements" present and their decay rates.

On the other hand common lead contains the following *four* isotopes: Pb^{208}, Pb^{207},

Pb^{206}, Pb^{204}. The 204 isotope is *not* the end-product of any known natural or artificial decay series. As a first approximation the proportions of these isotopes are the same for all samples of "common" lead.[2] Accordingly, if we take a sample of lead extracted from a radioactive mineral, and determine the ratios of the lead isotopes, the amount of Pb^{204} found will enable us to compute the common lead content.

There are, at present, certain limitations on this method. First, a considerable sample of lead is required. Dr. Nier has advised the writer (9) that he needs 10 milligrams of lead salt for convenient operation, and hence 20 or more to provide for the possible need of duplicate runs, but hopes soon to be able to use 1 milligram. It is not often possible to isolate 10 milligrams of lead in a pure form from the quantity of a given radioactive mineral available, and occasionally even less than one milligram is at hand.

Second, it is at present necessary to have the lead in the form of a rigorously pure lead compound, free from all other elements, especially those having isotopes that might be confused with those of lead. Nier's published work has nearly all been done with lead samples purified by the methods of atomic weight determinations. The most suitable form for the lead to be in is the iodide—PbI_2. Since bromine in traces is present in all so-called "C.P." iodine, and the combinations $I^{126}+Br^{80}=206$ and $I^{127}+Br^{80}=207$, it is essential to prepare the PbI_2 from specially purified iodine. The organic compounds lead tetramethyl—$(CH_3)_4Pb$ or lead tetraethyl—$(C_2H_5)_4Pb$ have sometimes been used for mass-spectroscopy, but here hydrides are formed, and one cannot distinguish between, say, Pb^{207} and $Pb^{206}H^+$.

Thus it is essential to have this part of the work done by persons who are fully conversant with the neccessities of the case, and the processes should not be entrusted to relatively untrained workers. It may be said that experiments are planned by Kulp (10) and others to see if some of these time-consuming steps can be avoided.

[2] Actually, since all rocks carry uranium and thorium in minute amounts, there will be a very small amount of radiogenic lead in common lead, but the quantity is so small as to have but a second order effect on the argument. See ref. (8) (e).

MEASUREMENT OF ISOTOPE RATIOS

The apparatus and technique for measurement of the isotope ratios have been described by Nier (8a–e). The apparatus is a complex and delicate piece of physical equipment, which needs to be operated by, or at the very least under the immediate supervision of a competent mass-spectroscopist. The commerical instruments are in general not adaptable to this type of measurement. When properly carried out, the results are accurate to 1 or 2 parts per 1,000.

The method of computation of the common lead correction is given in Nier's papers, and also in several papers by A. Holmes (11). Furthermore we can check the age found from the chemical analysis, corrected for the common lead content by the following four ratios:

A. Pb^{206}/UI
B. Pb^{207}/AcU
C. Pb^{208}/Th
D. Pb^{207}/Pb^{206}.

This last can be used because the decay rates of UI and AcU are not the same (1).

Owing to a variety of reasons exact agreement of age has not been found in all cases. In a number of instances the Pb^{208}/Th ratio gives variant results when the thorium content of the mineral lies within certain limits. This case is probably due to the less accurate methods available for the analytical determination of thorium, as previously noted.

Several determinations have been made where the agreement in ages for the different ratios is good. These are the ones used as fundamental points on the absolute time scale. The most recent discussion is by Holmes (11b). The over-all accuracy of these ages is of the order of units of millions of years. Other things being equal, accuracy is greater the older the age, because the value of the ratio is greater and because a given error has a smaller effect on its value. It should be apparent that no hard and fast rule can be laid down that will apply equally to all the better determinations. Holmes (11a) estimates that the earliest Precambrian ages (c. 2,000 million years) are known to within $\pm$ 10 million years. The writer considers that the absolute age for the (presumably) Upper Cambrian Kölm of Westergøtland, Sweden is probably 435 $\pm$ 12 million years.

FRESHNESS AND SUITABILITY OF THE SAMPLE FOR ANALYSIS

Finally we come to what is historically the final step but which should be the first question to consider when a new radioactive mineral sample turns up: is the particular specimen "fresh" or otherwise suitable for use as an age index? It is obvious that if leaching, enrichment, or weathering processes have removed or introduced any appreciable quantities of lead, thorium, or uranium, the specimen is of no value. It is also essential that radioactive equilibrium has remained virtually undisturbed since the mineral was first crystallized. These sound like very difficult requirements to meet, which they are, but proper studies to determine the suitability of a given specimen are not difficult to carry out. Unfortunately such studies have not always been made, and a great deal of time has been wasted—some of it valuable—by the neglect of these precautions.

A trained mineralogist can distinguish in the field the gross symptoms of unsuitability, such as a dull lusterless surface extending into cleavage faces, the powdery alteration products similarly situated, hydrated secondary mineral particles scattered through the main mass. Parenthetically it may be said that weathering or secondary mineral crusts that do not penetrate a specimen can be removed, leaving virtually fresh material in many cases.

In the laboratory the first step should invariably be the taking of an autoradiograph. Directions for this process are given by Marble and by Yagoda (12). Not only does this procedure give valuable information as to leaching, enrichment, movement subsequent to crystallization, inclusion of nonradioactive minerals, and variations in radioactive content, but also can furnish a qualitative estimate of the radioactive content. If it is then thought worth while to proceed with the analysis, etc., the existence of radioactive equilibrium can later be checked, if need be, using methods described by Wickman (13). A high degree of hydration is always a sign of alteration and of the lack of radioactive equilibrium. Minerals like autunite, torbernite, carnotite, tuyamynite are unsuitable age indices, using existing techniques.

It may be pointed out here that we have been speaking of the constancy of composition, etc. of a mineral since the time of its first crystallization. It is of course a fact that a mineral may, and undoubtedly does take a long period of time to crystallize out from solution or from magma, just how long is highly uncertain. It further takes a considerable period of time for a lens of kölm to be deposited. However, the times concerned are very short compared with the over-all errors of some 10 to 12 million years in our method, so that it is in order to consider the crystallization of a radioactive mineral virtually as an instantaneous process.

STRATIGRAPHIC RELATIONS

In conclusion, it was stated at the beginning of this paper that no discussion would be given to the very important and very difficult question of the relation between the absolute age obtained from a radioactive mineral in a pegmatite or mineral vein and the age in terms of sedimentary sequences. This is a question for the structural or the igneous geologist, not for a simple analytic chemist. But, as was pointed out in the previous paper by Mr. Hembest and as you all know, it is often many miles from a pegmatite to the nearest diagnostic fossil and, even if they are near each other, the field relations are usually obscure.

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SIGNIFICANCE OF THE STRATIGRAPHIC DISTRIBUTION OF BRACHIOPODS

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ABSTRACT—A survey of 1,200 genera of brachiopods to determine the distribution in time and the evolutionary pattern of the rise and decline of groups reveals that different kinds of patterns have occurred. The one in which a monophyletic stock gives rise to offshoots at a fairly uniform rate is called the "spindle pattern." That in which proliferation of genera is multiple and accelerated is called a "burst pattern" and is found to be the prevailing type. An artifact in all of the patterns is called the "monographic burst"; i.e. the exaggeration introduced by more intensive or comprehensive studies of some parts of the stratigraphic or biologic record than others. The survey shows that the history of the brachiopods is characterized by evolutionary bursts and that these are distributed in time serially and without very clear relation to the geologic periods. The bursts also show considerable provinciality and the force of intrinsic as well as environmental factors in their history.

INTRODUCTION

IN THE following survey of the distribution of the brachiopod stocks in time, we are concerned mainly with presenting an impartial picture of present knowledge. We have used over 1,200 genera in the construction of our charts which includes almost every genus known to the senior author up to September 1949. The evidence arrayed is not of a selective nature. No attempt is made to determine whether any of the genera are synonymous; nor is graphic representation made for splits that quite obviously can be made in genera according to present principles. Splitting, according to present information, is an integral part of a major classificatory revision, and is beyond the scope of the symposium. Many inferences are scattered through the text but they seem reasonable judgments to us on the conceptions or misconceptions that have arisen from certain features of brachiopod distribution.

The inferences that are offered will bear on one of the motives of the symposium, which is to find out whether the geological distribution of a group of organisms shows that life has been subjected to bursts of evolution and if so, whether there is any pattern to these bursts. Does the distribution of any one class in time, or of the entire animal kingdom indicate that life was subject to a periodic increase in the rate of evolution? Or was the group development such that bursts were scattered sporadically throughout its history, and with no apparent relationship to time or space? As far as the brachiopods are concerned, present evidence points to the existence of bursts in almost all stocks. How true a reflection of the actual history these bursts are will be discussed below, but no doubt exists that with the possible exception of the Permian and Pennsylvanian they show no periodic coordination. On the contrary, if the orthoid history, which is here discussed in detail, is representative, the greatest development of a burst is local in time and space.

The two extremes of interpretation, namely a lack of pattern versus a well defined one, is strongly reminiscent of the well established controversy confirming or refuting the existence of periodic and widespread diastrophism. The development of brachiopods is apparently not related to any of the so-called major periods of diastrophism. In many instances various brachiopod stocks seem to be limited sharply by systematic boundaries, but it must be remembered that systems are mainly defined on a paleontological basis.

We do not deny that diastrophism had any effect whatsoever on the development of the brachiopods. It is obvious that environment is a prime selective factor in determining the nature, extent and rate of speciation. Even minor changes of land and sea relationships such as the variations in

character of detritus carried by a river, the change in direction of currents and minor submarine faulting have far-reaching effects upon the extremely complex and delicate balance between organisms and their habitats. All such changes, whether major or minor, are ultimately dependent on diastrophism in the wide sense, but as yet, we cannot point to actual examples of direct influence and we certainly do not find close correlation between bursts and major earth movements.

METHOD OF APPROACH

Before presenting the evidence which leads us to make these statements, it is necessary to describe our methods of using the data at our disposal. A topic of this nature may have many different approaches, all of them with the same end in view. The main problem is to arrive at a practical interpretation of the concept contained in the term "evolutionary burst," and to determine means for measuring such an occurrence taxonomically, so that subjectivity is eliminated as far as possible.

A "burst" is generally accepted as implying a speed up of evolution and in this light may be defined simply as acceleration of stock diversification *relative to the previous history of that stock*. In terms of modern biological thought, there are many implications to this definition. To begin with, it means that a stock will pass from a genetically stable phase to a genetically unstable one (pedomorphic changes are just one example of this instability) during which time the stock will enlarge itself by the establishment of a series of independent divergences, which eventually become *stabilized*. We also know that even in the normal process of speciation, environment is a potent selective factor and will promote any genetic tendency to this end. In view of the increased rate of evolution that a burst portrays, it is logical to infer that concomitant with the phase of genetic instability, environmental changes occurred that were detrimental to competitors and that opened up new and varied habitats for the stock in question.

To paleontologists, who are at liberty to examine only the gross products rather than processes of evolution, stock diversification means morphological variation in hitherto stable characters that subsequently become stabilized to form new and independent lines of descent. A burst will therefore result in the relatively rapid expansion of a stock in time through the establishment of a number of contemporaneous divergences that show persistent morphological differences. It does not necessarily mean a greater spatial spread of the stock than before the burst occurred, although this is almost invariably true. In short we have to look for certain grades of morphological differences which will give an effective but correct picture of divergences if and when they occurred in the geological record.

If we accept the fact that grades of morphological differences between groups is directly proportional to the various categories of classification, the scale of the divergences will depend rather closely upon the rank of the taxonomic unit taken as a standard unit of measurement.

The conditions will not be satisfied by plotting sudden increases in numbers of individuals comprising a population. Sudden increases of this sort often reflect changes in environment in favor of a particular stock. The resultant population pressures through radiation may contribute to spatial spread and divergence but this is no more than a possible cause and is no measurement of effect.

The species could fulfill all the requirements of a standard unit, for speciation is the fount of all major divergences. Much of it however is abortive and cannot be assessed paleontologically. Moreover, in contrast to zoological systematics, the species at present is the most highly subjective unit in paleontological taxonomics. The number of species making up a stock will depend more on the amount of research done in faunas and on the personal opinions of the researcher than in a higher category. We feel that if the uneven quality of specific discrimination is considered in addition to the very large number of species involved, the result of using them would obscure rather than clarify any relationship that exists between bursts and geological time.

For a study of this kind, the genus is best suited as a basic unit. It is more objective than the species, and at the same time is wide enough in its morphological definition

to include forms from many parts of the world as against the tendency to regard the species as having only a regional spread. The number of brachiopod genera is not overwhelmingly large and yet as units they are small enough to show the more subtle type of divergences which would be lost if some higher rank were used. Moreover paleontological genera are records of the more successful type of divergences and thus illustrate quite effectively the more significant bursts, if any, that have occurred.

There are limitations in the use of genera in this capacity. The varying interpretation of what changes necessitate generic recognition has resulted in a lack of uniformity. What some conservative workers consider as a genus would be split into a number of genera by others. In addition to this, there is a tendency for paleontologists to work on faunas from distinct horizons or on stocks of a pre-determined range. This has had unfortunate repercussions on paleontological systematics. Certain segments of stocks have been subjected to detailed study and numerous splits arising from such investigation have been given systematic recognition while other segments have been ignored. These neglected genera are treated from a systematic standpoint as they were a hundred or so years ago. Consequently, it is probable that many are now conspicuously artificial. The other disadvantages to be considered would pertain also if any other rank were taken as a unit of measurement.

Despite the fact that many thousands of brachiopod species have been described from all parts of the world, and from much of the stratigraphic column, vast gaps still occur in our knowledge. In a generic study of the stropheodontids of North America and Europe, recently completed by Williams, it is estimated that the history for at least one third of the stock is unknown and that the history of a sizable amount of the remainder is inferred from a study of small numbers of specimens. When we consider that this is the story for the two best investigated regions in the world, and for one of the better known brachiopod families, the insufficiency of our data can be appreciated. These gaps are not only temporal and spatial but genetic as well. We can say by morphological comparison that a genus belongs to a certain family, but precisely when, and from what stock it arose is largely a matter of conjecture. This prompts us to use block diagrams rather than phyletic trees to represent brachiopod history. In this way, we do not commit ourselves to any phylogenetic preconception.

Because we have concerned ourselves with the representing of the distribution of brachiopod genera throughout the geological column and throughout all parts of the world wherever they have been recorded, the resultant charts do not pretend to be last word in correlation. Wide deviation must be expected from what were the actual time and space relationships between stratigraphic horizons from continent to continent, or even within smaller regions. In view of this we have accepted the data at their face value. In many instances no more is known about the range of a genus than, for example, that it occurs in the Devonian or the Jurassic. In other cases, e.g., Ordovician and Silurian brachiopods, it is possible to plot a more definite range. In the construction of the superfamily chart, therefore, we have done no more than divide each system into upper and lower, and plotted the genera accordingly. In the analyses of two of the better known superfamilies, the genera are recorded fairly exactly on the time scale, but even so, we do not claim that this is more than a rough representation of the actual stock histories. In only a handful of genera do we have the preservation of what might be transition stocks from one divergence to another (e.g., *Sulcatostrophia* Stainbrook) so that we can date with a fair degree of certainty the origin of a genus. In most cases the range of a genus is given from its first appearance to its disappearance in a particular region which may or may not represent only a small segment of its actual existence in time.

The last notable disadvantage to be discussed in our method of representing evolutionary bursts and the one which offers the strongest reason for accepting with considerable reservation the results of a study of this kind, is that we know nothing at present about the actual time involved in the establishment of a series of divergences. Although we have at our disposal a very rough calculation of the duration of each

system based on radioactivity measurements, we shall probably be criticized for representing all systems as having existed for the same length of time. There is no doubt that our charts are distorted in this respect; e.g., the Cambrian lines of brachiopods should probably be over three times as long as the Pennsylvanian but this will not alter the fact that 66 brachiopod genera are recorded in the Cambrian as against 63 in the Pennsylvanian.

To obtain some evaluation of the rate of evolution, Simpson and Newell are using the ingenious method in this symposium of plotting the number of new genera originating in a system against the calculated duration of the system, thus in the Cambrian 66 new genera arose, against 28 in the Pennsylvanian, which in the time ratio of 3:1 gives a somewhat higher rate of brachiopod divergence in the Pennsylvanian system. Such calculations, as these authors have recognized, can be misleading and may be very wide of the truth. Referring back to the Cambrian-Pennsylvanian comparisons, it is possible that the 28 Pennsylvanian genera originated at a uniform rate throughout the system whereas all the Cambrian genera originated in a tenth of the time assigned to the system. On this basis the rate of divergence in Cambrian times was eight times as great as that in the Pennsylvanian.

In short we shall not be in a position to obtain workable generalizations on evolution rates until we can determine precisely when a divergence first originated and how long it existed. Thus in figure 1a, an orthid burst apparently took place in the upper Canadian, and again in the lower Black River, an impression accentuated by the attenuation of the stock in Chazy times. This attenuation however could be filled in if some generic stocks of burst *A* migrated from American seas during Chazy times and if some generic lines of burst *B* originated elsewhere but populated the American seas during early Black River time. There is some evidence for this contention. Moreover the bursts would be less startling if the time interval from upper Canadian to upper Black River were represented in figure 1b, as twice as long as that represented in figure 1a, and if the exact point of origin for a generic divergence were to be plotted against the true time scale. On that basis, a burst, such as that in the Lower Black River, could be resolved into a more normal rate of development (fig. 2).

PATTERNS OF DEVELOPMENT

During our compilation of the charts we were impressed by the fact that virtually all the brachiopod groups can be referred to one of two fundamental patterns of development, which, for convenience, are termed "spindle patterns" and "burst patterns." An exception is represented by the almost "straight line" pattern shown by a few superfamilies such as the Discinacea and Craniacea which are represented by a few long ranging genera.

The "spindle pattern" (fig. 3a) is the one that is often used in idealized diagrams of stock ranges, and theoretically is the "normal" form of development in which a monophyletic stock will give rise to divergences at a more or less uniform rate to reach a climax, after which the lines of descent will be gradually reduced by extinction to just a few generic stragglers. This, surprisingly enough, is not the prevalent type of development in brachiopod history, the burst pattern being the more common. The climax in a stock history is here taken to be the time at which the greatest number of genera belonging to that stock existed. On this basis the essential difference between a "spindle pattern" and a "burst pattern" is that, in the former, the climax was attained well on in stock history while in the latter it occurred during the early stages of development.

Many brachiopod groups were initially or at subsequent stages in their history represented by a few stocks which suddenly burst forth into a variety of short lived genera. This acceleration of the rate of divergences gives rise to a characteristically swollen node (burst pattern, fig. 3b) contrasting with the more moderate proportions of an average line of descent. In most instances the entire stock comes to an apparently abrupt end (truncated burst, fig. 3b at XX). Now it is possible that when close studies are made of the ranges of stocks involved in truncated bursts, it will be found that extinction of all lines of descent was not simultaneous, but was staggered over a

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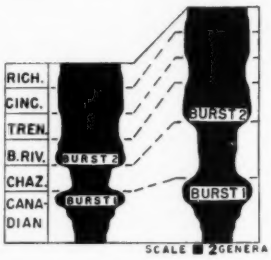

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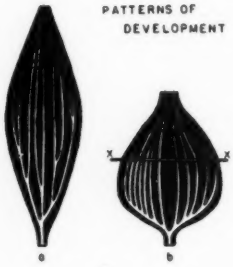

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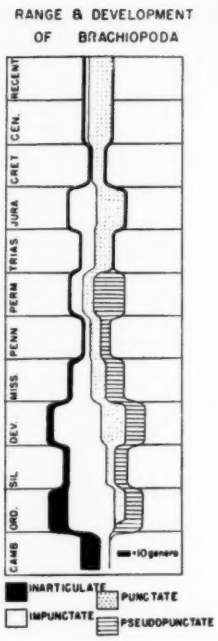

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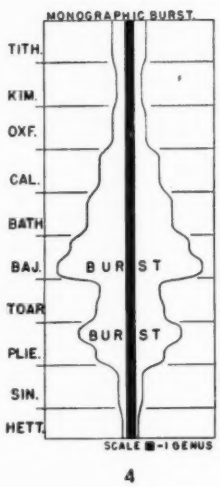

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FIG. *1*—The distribution of the American Orthacea in the Ordovician as it appears when time units are considered equal and when the time units upper Canadian to lower Black River inclusively are considered to be twice as long as the others.

FIG. *2*—Generic divergences forming a burst pattern (a), and a spindle pattern (b) in which the time involved for the establishment of the divergences is 3 times as great as in (a).

FIG. *3(a)*—A spindle pattern formed by a "normal" divergence rate. *3(b)* a burst pattern formed by an accelerated divergence rate. Extinction of all stocks at XX will form a truncated burst pattern.

FIG. *4*—A monographic burst. The distribution of the British Jurassic rhynchonellids in time. The median line represents the generic status of the group before the publication of Buckman's researches.

FIG. *5*—The range and development of the Brachiopoda in time, divided according to shell structure.

period of time that is relatively short compared with an accelerated conclusion to the spindle pattern climax. Even so, the feature is unusual and possibly indicates obliteration as a result of widespread environmental changes, or of genetic causes inherent in the stock as a whole such as gerontomorphism. The probable answer is a combination of both with an emphasis on the latter because it is difficult to picture environmental changes being inimical to a stock that had already become diversified and adapted to a variety of conditions. In some brachiopod groups, such as most of those originating in the Cambrian,—the Dalmanellacea and the Plectambonacea, many genera appear for the first time at about the same horizon and thereby give a truncated base to the patterns of development. We do not consider this the result of a natural phenomenon but the result of insufficient paleontological work.

One other term which we have adopted remains to be explained, namely "monographic bursts." Some of the bursts have an obvious artificiality due to intensive systematic splitting in one particular segment of stock history as opposed to a very conservative treatment of other segments of the same stock. As an example of this we have figured the rhynchonellid burst of the Jurassic (fig. 4) which is in the main artificial. Up to 1914, one genus only, namely *Rhynchonella* Fischer covered the entire range of Jurassic rhynchonellids. In that year Buckman (1914) proposed 41 Jurassic rhynchonellid genera, distributed as in figure 4. His splits were based upon supposed genetic development of ornamentation and folding of the anterior commissure. In this study we are not concerned so much with the validity of these splits as with making

a few observations, which, if true, would change the entire pattern.

The distribution diagram shows two bursts, one in the Upper Pliensbachian and the other in the Bajocian, but the study was based almost entirely on English rhynchonellids. Accordingly the Toarcian attenuations as well as others could represent the migration to areas outside of the British regions of established genera. The apparent bursts correspondingly indicate an invasion of genera which originated elsewhere. Furthermore the pre-Hettangian attenuation is quite unreal for the Triassic is crowded with rhynchonellids as varied as those of the Jurassic and it is our belief that the Jurassic forms represent a climax to a diversification that started in the Triassic at least.

The senior author is of the opinion that most bursts are artificial and that they are the product of insufficient paleontological research, and that when more data are available, the spindle rather than the burst pattern will prove to be the normal type of development. The junior author agrees that many of the burst patterns illustrated here can be expected to undergo radical modification under the impact of new data. Nevertheless these differences between the spindle and burst patterns are ultimately related to rates of speciation which in turn are due to the interaction of mutation rates and environment changes. Repeated spindle patterns would therefore imply approximately uniform rates of mutations and environmental changes, conditions hardly to be expected throughout all geological time, so that bursts as manifestations of acceleration of these rates are to be anticipated.

HISTORY OF THE BRACHIOPODA

We can now turn to a critical examination of the history of the Brachiopoda based upon the number and range of genera. We have presented the evidence as it appears on three planes of classification, namely at class level, at superfamily level and finally at the family level for two of the better known superfamilies. By this means we hope to obtain some viewpoints which would not come to light were we to limit ourselves to one level or another.

Figure 5 is a composite diagram of the brachiopod phylum in time, divided on the basis of shell composition and structure. The group began in the Cambrian with a truncated base attributed to incomplete knowledge of stocks of those times, and rapidly attained a climax in early and middle Paleozoic times (221 and 233 genera in the Ordovician and Devonian, respectively). From then on the group dwindled unevenly being represented today by 68 genera. Only the inarticulate and impunctate lines are represented initially. The former group has waned since Ordovician times. The great burst of the latter was in the Lower Paleozoic and after a Mesozoic revival, which may be exaggerated as now represented, they have dwindled to a few genera in the modern seas.

Our knowledge of the first differentiation of the punctate and pseudopunctate brachiopods is very small. Present indications point to their origin in late Cambrian or early Ordovician times from what must have been an impunctate root. After a burst in the lower Devonian the punctate stocks declined but revived with a second burst in the Mesozoic and have continued to hold this dominant position to the present day. The pseudopunctate history is remarkable for the truncated burst the stock underwent in the Permian. In post-Paleozoic times the group may be represented as an insignificant line by *Thecidea* and allies, representatives of which still exist.

In figure 6 the evidence recorded above is presented as the distribution in time of the 23 superfamilies into which it is now possible to divide the brachiopods. We do not intend discussing the details of all superfamilies, but we will point out some salient features of the development as a whole and the course of evolution of certain of the more familiar groups.

Perhaps the most striking impression given by this distribution is that in the articulate brachiopods, the spindle pattern is entirely subordinated to the burst pattern, but in the Inarticulata, the burst pattern does not occur. In the latter subclass, every superfamily with the exception of two is represented by only a few genera and has either a very short range (e.g. Rustellacea Paterinacea, Kutorginacea) or an extremely long one (e.g. Discinacea and Craniacea). There are indications that the group as a

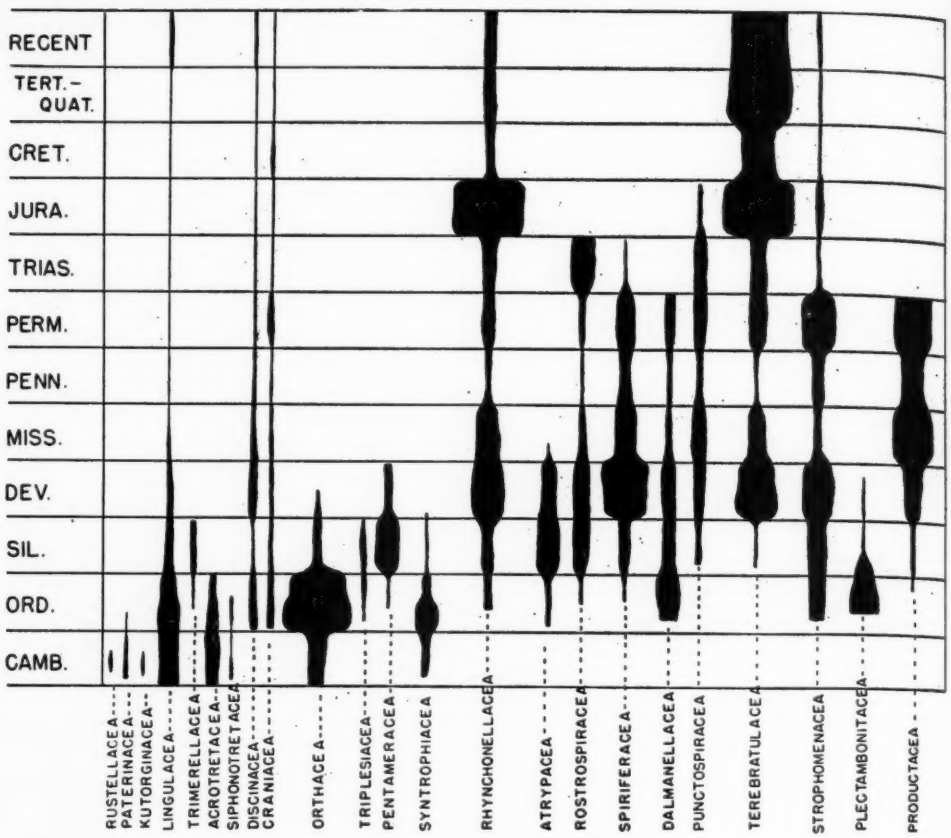


FIG. 6—The range and development of the superfamilies of Brachiopoda in time. The thinnest line drawn (e.g. Pennsylvanian to Tertiary Lingulacea) equals one genus.

whole was subject to a greater variation than the chart shows but what effect systematic research on them will obtain is unknown. The two exceptions, namely Lingulacea and Acrotretacea were subject to a number of divergences in Cambro-Ordovician times, represented by maxima of 19 genera in the Lower Ordovician and 12 in the Upper Cambrian respectively, but the truncated bases of both stocks indicate much new material has yet to be collected from the Lower and Middle Cambrian and suggests that both will probably conform to the spindle pattern.

Among the Articulata, the spindle pattern in an unmodified form is displayed only by the Triplesiacea and the Punctospiracea, both minor superfamilies embracing less than 4% of the total brachiopod genera. In the Pentameracea, Syntrophiacea, and Atrypacea, it was modified by the superimposition of a minor burst pattern during Silurian, Lower Ordovician, and Silurian times respectively. Rostrospirids conform to the pattern during their Ordovician to Mississippian history but Pennsylvanian descendents gave rise in Triassic times to a truncated burst. Finally the plectambonitids may also show a spindle pattern of development when their Lower Ordovician and Upper Cambrian (?) history is fully known.

Significant burst patterns are a feature of many superfamilies viz. Orthacea (in the Ordovician), the Pentameracea (Silurian), Rhynchonellacea (Devonian to Jurassic), the Atrypacea (Silurian), Rostrospiracea (Triassic), Terebratulacea (Devonian to Jurassic), (?) Strophomenacea (Permian), and Productacea (Mississippian to Per-

mian). There are indications however that many of these patterns will be modified as systematic work progresses. The Orthacea for example here include the clitambonitids which were given superfamily status by Öpik. It is believed that this great burst will eventually assume more moderate proportions.

Above, we described the Jurassic rhynchonellid burst as largely monographic. The Devonian bursts of this stock could be similarly explained. The Devonian rhynchonellids have recently received intensive treatment by German paleontologists, yet the Silurian is crowded with rhynchonellids. We believe that future work will taper the Devonian bursts and transplant many of the divergences to the Silurian or even earlier because, during the compilation of these charts, new data from the publication of Wang's study (1949) of the Maquoketa brachiopods produce a definite Ordovician node in the rhynchonellid line.

The development of the Terebratulacea can be interpreted in a like manner except for the Devonian forms which, as Cloud (1942) has demonstrated, were apparently the product of a series of true bursts with a maximum in Oriskany times. Throughout the remainder of the Paleozoic the Terebratulacea are represented by a comparatively few stabilized lines, but the Mesozoic saw a second burst, greater than the Devonian one, which established the stock as the dominant one today. The patterns of development throughout the Mesozoic are not true reflections of the actual terebratuloid history. The Jurassic burst is mainly monographic for the Triassic contains many terebratuloids that have not been subjected to the intensive study of those in the Jurassic. Moreover, the Cretaceous attenuation is due to neglect of the numerous and diverse terebratellids of Europe.

Conspicuous truncated bursts indicating late divergence in stocks followed by a complete extinction of the resultant lines of descent are exhibited by the Rostrospiracea, Dalmanellacea, Productacea and probably the Strophomenacea. The pattern for the Rostrospiracea is almost the ideal spindle until the Triassic when a burst of generic divergences occurred, all of which became extinct before the Triassic ended. The dalmanellid history is comparable. Making allowances for the truncated base, the lower and middle Paleozoic dalmanellids showed a spindle pattern of development scarcely modified by a lower Middle Ordovician burst. Stock attenuation that continued from the Mississippian to the Pennsylvanian was however arrested by a Permian burst representing *Enteletes* and allied genera which did not survive the Paleozoic. The Productacea started modestly with the chonetids of the late Ordovician and burst into conspicuous divergences in the Devonian. Descendants of these lines flourished until Permian time when they all suffered extinction. The pattern of strophomenid development is similar but is complicated by the appearance of the Thecideidae, those supposed aberrant strophomenids of Mesozoic to Recent times. The Strophomenacea originated in early Ordovician, possibly Late Cambrian times and progressed gradually to the Devonian, when the stropheodontids reached a climax. The stock became drastically attenuated during the Mississippian and Pennsylvanian periods, to culminate finally in the glorious burst of the orthotetids, all of which, with the supposed exception of a few hardy survivors (Thecideidae), died out by the end of the Permian.

It is interesting to note the coincidence of three lines of truncation with the close of the Permian. We have already discussed theoretically the causes that could result in truncated burst patterns, and at this juncture it seems opportune to expand somewhat on these conclusions. In each of the three stocks that disappeared viz. the Strophomenacea, Productacea, and Dalmanellacea, the bursts resulted in the appearance of bizarre forms, products of gigantism and high specialization. The Strophomenacea included such forms as the rudistid-like *Scacchinella*, the cemented *Meekella*, and the gigantic *Derbyia*; the Productacea produced specialized forms like *Yakovlevia*, and *Richthofenia* and gigantic forms like *Waagenoconcha*; and the Dalmanellacea, *Parenteletes*, and *Entelletella* with complicated internal structures. It is an odd fact too that coarse plications of hitherto smooth genera occurred all over the world at about the same time. The fundamental mor-

phology for most of these forms was achieved, not in the Permian but during the Mississippian and Pennsylvanian and it is possible that one of the strongest selective forces that gave direction to such trends was some world-wide change in environment, perhaps changing salinity brought about by the growing ice caps of the great glacial era that had set in. It is also possible that the resultant over-specialization and phylogerontism conspired to make it impossible for the three stocks discussed to survive any subsequent environmental changes (e.g., a return to a more normal salinity when glaciation came to an end). Inasmuch as five other contemporaneous but less specialized groups of articulates (viz. Terebratulacea, Punctospiracea, Spiriferacea, Rostrospiracea and the Rhynchonellacea) did survive the ecological upsets of the Permian, causes other than salinity changes must be sought to explain the extinctions discussed above. Overspecialization seems to be the most reasonable.

A last point to be made in respect to this chart is that not only were there no bursts during the Pennsylvanian but also that many generic divergences established during Mississippian or pre-Mississippian times died out so all stocks became attenuated. This impression may be a false one and a reflection of our lack of knowledge or a lack of intensive work on the brachiopods of this period. On the other hand Pennsylvanian conditions such as glaciation or the effect of the widespread coal swamps may have been inimical to many existing groups as well as to the initiation of many new diversifications.

It now seems relevant to examine certain selected groups in more detail to determine whether bursts are evident at a family level and whether they have more than a local or regional significance. For these purposes, the Orthacea (including Clitambonacea) have been chosen as an example of the burst pattern and the Dalmanellacea as an example of a modified spindle pattern ending in a truncated burst. Both groups have recently received fairly thorough modern treatment in North America and Europe and thus provide fairly exact objective data as well as an opportunity to determine the spatial significance of divergences.

When the orthoid burst is split up into families, the resultant patterns assume more moderate proportions. Thus in the chart drawn from American data only (fig. 7) the Plectorthidae and the Dinorthidae approach the burst pattern, the former being also a good example of the truncated burst. The Orthinae might belong to this class but the truncated base casts some doubt on assignment to that pattern and suggests that it might be more typical of the spindle development. What is most striking is the large number of short ranged stocks; about 65% of the seventeen family stocks here originated, and were limited to, or had their main development in the Ordovician. This statement is also true for the European Orthacea (plus Clitambonacea) (fig. 8): 85% of the fifteen family stocks recorded are limited to or mainly characteristic of the Ordovician and only two of the stocks viz. Orthinae and Clitambonitidae underwent a burst development.

Accordingly the burst of this superfamily was not in turn made up of a series of family or subfamily bursts, but consisted mainly of a large number of aberrant, short lived, and meagerly represented family stocks. Only a few retained the genetic plasticity of the protostock long enough to give rise to a burst of generic stocks when conditions for such divergences were favorable.

A comparative study of the genera making up the North American and European orthoid (s. l.) family stocks and of the time of maximum development for the various stocks (fig. 9) show other interesting facts. Most genera (actually about 73% of the total) are typical only of one region or another and in those cases where stocks lived in both regions at the same time, there is often no coincidence in time of the obtained maxima of the development. Thus, at present for example, the Protorthidae and Orthidiellidae are peculiar to North America and members of the Angusticardiniinae and Estlandiidae are found only in Europe. Furthermore the eoorthid and hesperorthid groups are found in both continents, but have no generic stock in common and have an appreciable difference in time of maximum development. In the Orthinae, of which just over 50% of the generic stocks are common to North America and Europe,

the time of maximum development was in the Lower Ordovician for the former region and in the Middle Ordovician for the latter.

We realize the shortcomings of taking just one, albeit a well known stock, as typifying the burst pattern and generalizing from the analysis of such data. Nevertheless, the conclusions are so closely accordant with current ideas on the process of speciation and spatial occupation by successful stocks that this is offered as an illustration of the pattern of events that may be expected during bursts of evolution. A burst consists of a series of specialized divergences the majority of which are short lived and so may fail to bridge some of the great ecological barriers that exist between the major habitats of the earth. The result is that the burst will have a regional rather than a continental significance. This will be accentuated by the fact that those stocks which successfully invade other regions will tend to undergo yet another but distinctly later series of short lived divergences which eventually result in the appearance of stocks very different from the parent line and showing only family or some higher rank of affinity with their closest related contemporaries in other regions.

A similar analysis of the Dalmanellacea will substantiate the ideas expressed above in another way. We have already commented upon the truncated base that was revealed by a composite diagram of that superfamily. Figures 10 and 11 show that four distinct family stocks made a simultaneous appearance in lower Middle Ordovician times. In view of the existence of these basic differences in the earliest recorded dalmanellids, it is certain that dalmanellid stocks earlier than those so far known existed, and that a spindle pattern of development could account for the present distribution equally well as a burst pattern.

An impressive fact is the long range of the dalmanellid families with the exception of the Heterorthidae, the problematic Paurorthidae and the aberrant Mystrophoriidae. Only three bursts are evident throughout the entire dalmanellid history, namely the Permian schizophorid burst of America

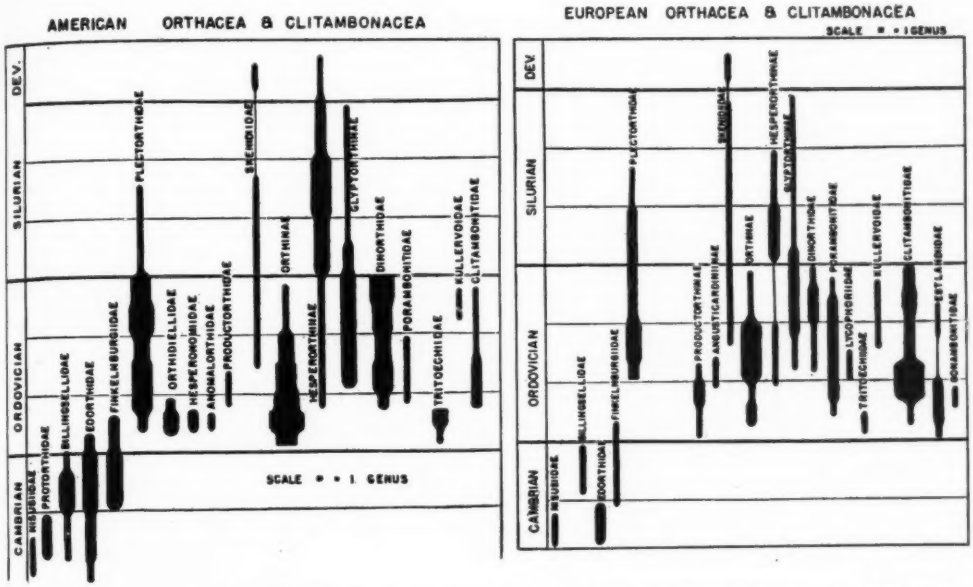


FIG. 7—The range and development of the American Orthacea and Clitambonacea divided into families and subfamilies.

FIG. 8—The range and development of the European Orthacea and Clitambonacea divided into families and subfamilies.

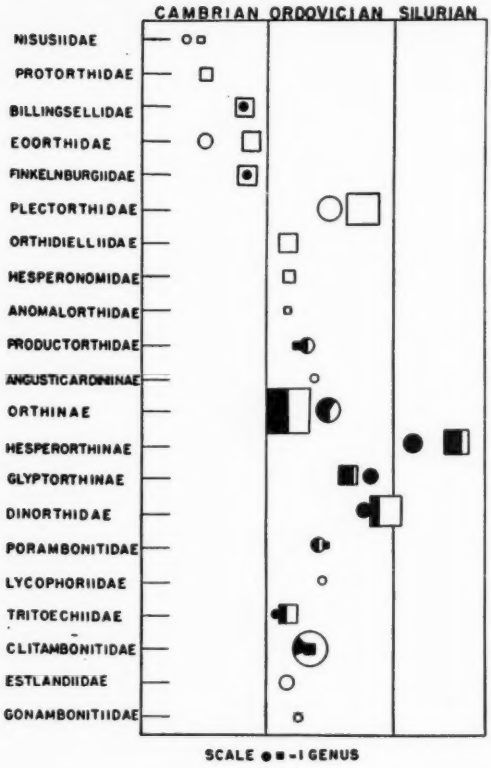
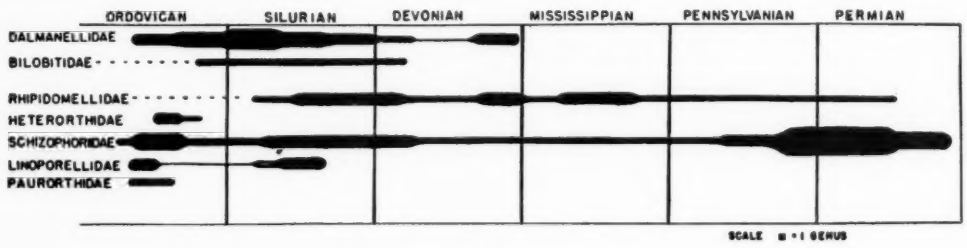


FIG. 9—A comparison in extent and time of North American and European climaxes, for the various families and subfamilies of the Orthacea and Clitambonacea. A square represents an American climax, a circle a European climax. Shaded portions represent the proportion of genera common to both continents.

with a lesser representation in Europe and the Middle Ordovician dalmanellid and heterorthid bursts in Europe, some members of which are represented in North America.

The last two bursts are especially significant for the production of short-lived generic stocks. Further, even considering these bursts and such locally significant divergences as those that originated during the development of the Rhipidomellidae (e.g. *Perditocardinia* and *Thiemella*), less than 50% of the genera were unique to one continent or the other, figure 12. In short, as far as the dalmanellids are concerned, bursts were responsible for a high percentage of spurious novelties of only regional significance, while the long ranging stabilized stocks which may or may not have



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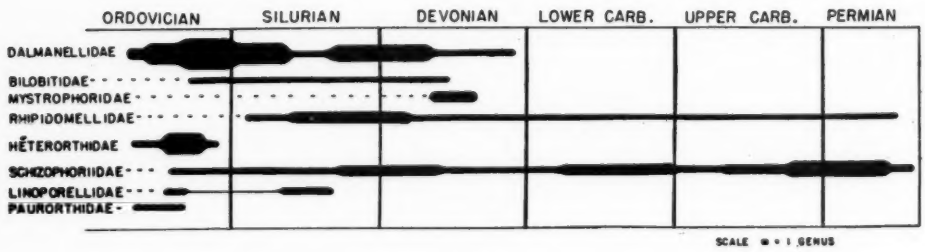

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FIG. *10*—The range and development of the American Dalmanellacea divided into families.
FIG. *11*—The range and development of the European Dalmanellacea divided into families.

arisen from bursts spread from North America to Europe or vice-versa.

CONCLUSIONS

In this necessarily rough and limited survey of the historical development of the Brachiopoda, existing but ample evidence shows (1) that bursts of evolution were important adjuncts to the whole process of diversification amongst the articulates, and (2) that bursts are scattered throughout time, except the Pennsylvanian-Permian periods, without any apparent periodicity. Evidence also indicates that the Pennsylvanian and Permian periods were times when environmental changes were drastic and widespread enough first to reduce the total number of brachiopod stocks and then to eliminate certain unrelated but overspecialized stocks.

That such parallelism in the stock histories of brachiopods differs from the patterns of development as they were formerly interpreted is apparently borne out by a detailed analysis of distribution of the Orthacea and Dalmanellacea in North America and Europe. If these two groups are representative of the lesser known superfamilies then it seems that a burst is a product of a major morphological change in an existing stock. (e.g., a pedomorphic novelty) which through rapid divergence gives rise to a series of widely different lines of generic or family status, most of which are short lived aberrant failures. The result is that bursts have a regional rather than a world-wide significance and even when migration from one region to another occurs, newly established groups tend to undergo development and divergence independently of the parent stock.

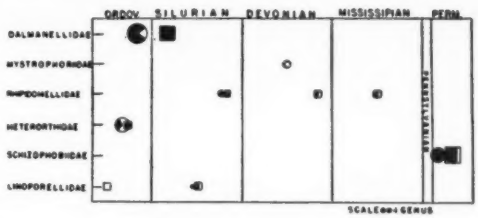

FIG. *12*—A comparison in extent and time of North American and European climaxes for the various climaxes of the Dalmanellacea. A square represents an American climax, a circle a European climax. Shaded portions represent the proportion of genera common to both continents.

What degree of truth is embodied in this survey has been discussed at length and there is no doubt that outside of some already obvious misinterpretations, the present ignorance of the actual time involved in the establishment and duration of the generic stocks considered here, and the uneven quality of systematic work have given many distorted pictures of facts. This study must therefore be accepted as an interim report on the conditions and limitations of our present knowledge; a true description of the history of the Brachiopoda and a plausible interpretation of the processes and course of evolution belong to the future.

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EVOLUTION RATES AMONG CRINOIDS

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ABSTRACT—The crinoids are especially well suited for study of evolutionary trends and rates because of the complexity of their skeletal organization, remarkable range of adaptive variations, long geologic history, and abundance of described species. The general nature of characters used in differentiating crinoid species and directions of evolutionary trends is described briefly. Data on stratigraphic and geographic distribution of species are presented in the form of graphs variously organized according to groups. These serve to provide both a general picture and an analysis of the amount of specific differentiation among the crinoids in different parts of the geologic record. Culminations in differentiation are marked in the Middle Silurian, Lower Mississippian, and Upper Jurassic. The observed distribution indicates that evolutionary rates actually fluctuate between wide extremes.

INTRODUCTION

FEW, if any, kinds of invertebrates offer better opportunity for study of evolutionary trends and rates than crinoids. Support for this assertion comes from several lines of appraisal. No other group of animals, including vertebrates, possesses a skeleton composed of such an enormous number and variety of elements as are found in some crinoids. In number, the ossicles may exceed 2 million separate parts belonging to a single individual. The variations in structural organization, shape, size, and special sorts of adaptations seem to be endless. Modern crinoids include forms living on deep ocean bottoms, forms solidly attached in wave-lashed shallow waters, and forms that are free-swimming. Abundant remains of extinct species are found in many Paleozoic and Mesozoic shallow water deposits and show adaptation to such environment. The crinoids range from lower Middle Ordovician to the present, and thus are exceeded in length of record by only a few groups such as brachiopods, nautiloids, and gastropods.

The variety of differences that are found in the form and structure of the fossil crinoids is expressed by a taxonomy constituting hundreds of genera and thousands of species. Naturally, variations occur within the limits of populations that are considered to belong in this or that species, and, although most collections lack an aggregate number of more than some hundreds of specimens that are included in any one species, actually many species undoubtedly included millions of individuals. Abundance of individuals is an element not to be overlooked in study of evolutionary differentiation and rates of evolutionary change, for prolific stocks are likely to contain largest number of divergent trends. Probably any great expansion in the population belonging to a species of animals is as noteworthy in the study of evolution rates as seeming abrupt increase in number of species; conversely, great dwindling of populations and decrease in number of species may be significant. Some thick formations are largely composed of crinoid remains, whereas others lack them, but no satisfactory means for quantitative measurement of such variations are at hand.

The yard-stick used for measuring evolution rates among crinoids in the study recorded in this paper is a scale calibrated in terms of number of species. Such a scale is a reasonably reliable tool for plotting fluctuations in the breadth of specific differentiation in successive epochs of earth history, but it furnishes only crude, indirect means of detecting and measuring significant accelerations or retardations of evolution rates. Further, adequacy of the source data obviously depends on several conditions which affect present knowledge. These conditions particularly include factors of discovery, state of preservation of collected fossils, and degree of completeness in research and publication on available fossil crinoids in the world. Discovery is important, as illustrated by the extent of our dependence on finds in a single East Indian

island (Timor) for knowledge of Permian crinoids; a few years ago, all collected Pennsylvanian crinoids put together probably would not total 400 specimens, whereas collections mainly obtained by intensive efforts in the mid-continent region now include not less than 20,000 specimens. We owe very much to the work of assiduous collectors of crinoids like Troost, Hall, Worthen, Wachsmuth, Springer, Rowley, and many others in North America, and to Quenstedt, Angelin, de Loriol, De Koninck, Jaekel, Bather, Wanner, Wright, and many other Europeans. If the crinoid localities at Kirkfield, Ontario; Crawfordsville and St. Paul, Indiana; Decaturville and neighboring places, Tennessee; Burlington and Keokuk, Iowa; Dudley and the Clitheroe district, England; Gotland; the Eifel; Lyme Regis; Holzmaden—if these and a dozen more like them were undiscovered, known crinoid species would be enormously fewer. State of preservation is important, for most collections contain fragmentary remains, badly weathered or otherwise damaged specimens, and various kinds of undeterminable crinoid material, which include traces of many undescribed species; this is quite certain. Degree of completeness in research and publication on fossil crinoids, measured in terms of collections available for study, is less significant as a factor in examining distribution of described crinoid species than in similar analysis of some other invertebrate groups, but it should not be overlooked.

The source data on crinoid species used in preparing graphs published in this paper have been compiled from indexes by Bassler & Moodey (1943), Biese (1934, 1935–1937), Biese & Sieverts (1937, 1939), and Sieverts & Biese (1939), supplemented by card file records based on later-published papers by several authors. Forms recorded merely by reference to genus and not to species, have not been included in tabulations, and specific terms considered to be junior synonyms of others likewise have not been counted. Although duplications are believed to have been avoided, there are doubtless some omissions—surely too few, however, to change any of the diagrams appreciably. The species have been classified in four groups, as explained in the figures, in order to show at least approximately the Old World or New World placement of species now known in each stratigraphic division. A genus is classed as Eurasiatic if none of its contained species is recorded from the Western Hemisphere (or, for all practical purposes, North America), and a genus is classed as American if no species referred to it occurs in Europe, Asia, Africa, or Australasia. Many genera are represented by species in North America and by other species in the Eurasiatic realm, as here defined, and these are termed cosmopolitan genera; American species belonging to these cosmopolitan genera are shown in one pattern and Eurasiatic species assigned to these same genera are shown in another pattern. The lack of cosmopolitan species in any of the cosmopolitan genera deserves notice, for the actuality of such complete separation seems *a priori* subject to doubt. Very few of the known forms of American crinoids can be interpreted as specifically identical to Eurasiatic forms. This condition seems to reflect evolutionary plasticity in the crinoids as a whole.

One qualifying factor, not so far mentioned, needs to be considered before proceeding to discussion of the nature and rates of crinoid evolution. This is the relation of sedimentary facies predominating in deposits of a particular part of the geologic record, in either or both of the hemisphere divisions. If, as in parts of the Mississippian (Lower Carboniferous) rock successions, sedimentary environments specially suitable for habitation by crinoids are shown to have been very widespread, abundance of species described in the literature is explained readily. Paucity of described species, as in Upper Silurian strata, reflects the generally unfavorable sedimentary environment indicated by character of these rocks in areas of their exposure on the continents; it does not mean that in undiscovered—possibly undiscoverable—parts of the world, crinoid species are similarly rare. Variations of these sorts are not true expressions of expansion and decline of crinoid abundance, nor of tendency to accelerate or retard evolutionary differentiation.

NATURE OF EVOLUTIONARY TRENDS

General pattern.—The purpose of this

part of the paper is not to describe evolutionary trends of crinoids, both because too much space would be needed and because at least partly this has been treated elsewhere (as Moore & Laudon, 1943; Moore, 1950). Merely an enumeration of the sorts of observed changes in form and structure of the crinoids is judged to be sufficient here to provide some comprehension of the characters that are chiefly influenced by evolution and are used in the taxonomy of the group.

A pattern of evolution that can be recognized in all main divisions of the crinoids is one that may be represented by a curve with ascending and descending limbs on either side of a more or less broadly rounded peak. The ascending part of this curve denotes generally increasing complication of structure, accompanied to some extent by expanding size, and by growing number of species. The descending limb corresponds to progressive simplification of structural features, with reduction or loss of parts, accompanied by diminishing average size of individuals and decreasing number of species. The peak of the curve marks acme of evolutionary differentiation. This is an over-simplified description, because several qualifications and some exceptions need to be stated. Peak development of most Paleozoic crinoids was attained in the Mississippian period and that of the later crinoids in the Jurassic.

Features of the calyx.—The crinoid calyx comprises parts of the organism above the stem, exclusive of free appendages. The calyx is divisible into dorsal cup and tegmen.

Evolutionary trend in shape of the dorsal cup is in the direction of lowering its height and developing perfect pentamerous symmetry. From steeply conical or high bowl shape, a discoid form, ultimately modified by deep basal concavity, is produced. The presence of two circlets or only one circlet of plates below the radials seems to be a fundamental structural character having significance in definition of ordinal and subclass divisions of the crinoids, and within the span of paleontological observation, evidence of evolutionary derivation of one type from the other is found nowhere. The lowermost circlet in all main branches of the crinoid assemblage, however, shows tendency to reduction in the number of plates by fusion, and this includes the Flexibilia, in spite of the remarkably stable three-plate plan of the lowermost circlet in that group. Evolutionary changes which have much importance in taxonomy affect the posterior interray area of nearly all crinoids. Herein are some fundamental distinctions which indicate cleavage of the camerates from other crinoid stocks before the beginning of the fossil record and lack of possible connection between camerates and articulates. The trend in all crinoids is toward simplification of posterior-interradius structures and their elimination from the dorsal cup.

The tegmen is much more variable and less regular in structural features than the dorsal cup. Some very primitive and also evolutionary end-product inadunates possess a tegmen composed of a single circlet of plates (orals), but most inadunates and all camerates have a many-plated tegmen which may be elevated in an anal sac or tube of various shapes and sizes. Flexible and articulate crinoids have a leathery tegmen which may bear disconnected small calcareous ossicles. Characters of the tegmen reveal evolutionary trends in some groups and are useful in definition of many genera.

Features of arms and pinnules.—The arms of a crinoid comprise all free appendages attached to the calyx except branchlets of the arms called pinnules. These parts exhibit surprising variation and complexity of form and structure, most of which is important in taxonomy and in study of evolution. Characters of form relate especially to the shape of arm plates (brachials) and the pattern of branching and pinnulation. Structural characters particularly include the nature of articulation between brachials, which may be muscular or ligamentous (half a dozen different types), distribution of the different categories of brachials and articulations, and placement of pinnules if present. The uniserial or biserial arrangement of brachials also is important. Evidence of several sorts indicates that the biserial type is derived by evolution from the uniserial, yet nearly all post-Paleozoic crinoids have uniserial arms.

Features of the pelma.—All parts of a crinoid exclusive of the crown (calyx, arms,

and pinnules) are collectively termed the pelma, a name made familiar by its incorporation in Pelmatozoa as designation for all attached echinoderms. The pelma includes the stem and its attachments, such as cirri distributed at intervals along the stem and the rootlike branches called the radix. The pelma also includes various special types of holdfasts, such as cemented disks, grapnel-like structures, and bulbous compartmented bodies. This part of the crinoid below the crown is hardly less varied in features of form and structure than the crown itself. Although somewhat neglected in paleontological research, it has importance in classification and study of evolution of the crinoids. The most common types of stem segments are circular disks, wafer-thin or thicker than wide, and solid except for a central perforation. Other stem segments are elliptical, quadrangular, pentagonal, stellate, or crescentic in outline, and some consist of five discrete parts which are joined along radial sutures. The shape of the central perforation is varied, and articular markings on surfaces of contact with adjoining segments are of several types, associated with different degrees of flexible ligamentous union. Most stems contain clearly differentiated nodal and internodal segments, the latter being classifiable in a number of subtypes. Taken all together, characters of the stem may outrank features of the crown in taxonomic usefulness, as is demonstrated for some Mesozoic crinoids.

The fact that modern free-swimming crinoids, the comatulids, lack stems in the adult stage—and likewise many Mesozoic and Cenozoic forms—does not mean that they are to be left out of consideration in connection with the pelma, for the centrodorsal plate with its attached cirri is partly derived from the vanished stem. Loss of the stem is also a product of the evolution of this group.

PALEOZOIC CRINOIDS AS A WHOLE

The oldest known crinoids come from Lower Ordovician or Upper Cambrian (Tremadocian) rocks of Wales, which contain undoubted inadunate remains (*Dendrocrinus*).

In Chazyan strata of North America the record begins with appearance of some 20 described species (fig. 1), of which three-fourths are camerates and the remainder inadunates. A supposed crinoid (*Trachelocrinus*) from Upper Cambrian rocks of Montana is actually a cystoid, and a small, well-preserved camerate crinoid (*Trichinocrinus*) from supposed Lower Ordovician (Canadian) limestone in Newfoundland is now regarded as belonging in the Chazyan. The upper division (Mohawkian) of Middle Ordovician rocks contains five times as many crinoids as the lower, and if these parts are added together, Middle Ordovician crinoids are twice as numerous as those found in the Upper Ordovician. Only a small fraction of the known Ordovician species are Eurasiatic and they are of Mohawkian age. Therefore, measured by species, Ordovician crinoids are predominantly American and peak abundance is in the Middle Ordovician.

The Silurian record shows very few crinoids in lower and upper parts of the system but an enormous expansion in the Middle Silurian. About 60 per cent of the described species occur in North America, but nearly four-fifths of all Middle Silurian species belong to cosmopolitan genera. Thus, expansion of the crinoids in the Eurasiatic realm and occurrence of many genera represented by species on both sides of the Atlantic are important changes, compared with the Ordovician. Also, Silurian crinoid species are more than three times as numerous as Ordovician.

In Devonian rocks, described crinoid species exceed those from the Silurian by approximately 100, but the peak which exists in the Middle Devonian is less prominent than that of the Middle Silurian. This is readily explained by the relatively large numbers of Lower and Upper Devonian crinoids (fig. 1). As in the Silurian, cosmopolitan genera contain most of the species.

There are nearly 1,600 species of crinoids in the Mississippian. This is well over twice the number of Devonian species. Peak development in the Mississippian system as well as in the Paleozoic as a whole is found in the Osagian, the upper part of the Waverlyan series, Lower Mississippian. Therein, the great bulk of the known species is American (fig. 1). No Eurasiatic species of Eurasiatic genera are recorded in Lower

Mississippian rocks, but they appear in the Upper Mississippian; as in older rocks, species belonging to cosmopolitan genera predominate over others.

The Pennsylvanian record of crinoids is now considerably larger than a few years ago, because many species have been described since 1938, but a considerable number of additional forms collected remain to be named. As matters stand, crinoids from this part of the Paleozoic succession are relatively few and they are almost exclusively American. Greatest numbers of species are from upper Middle Pennsylvanian (Desmoinesian) and lower Upper Pennsylvanian (Missourian) marine members of the cyclic sedimentary deposits of Kansas, Oklahoma, and Texas.

Permian crinoid species which have been described chiefly from Timor total approximately 325, as compared with a few less than 275 from Pennsylvanian rocks. Except for a few Lower Permian species from North America, the Permian crinoids are entirely Eurasiatic, approximately half of them belonging to genera which are unknown in the Western Hemisphere (fig. 1). Although a majority of the Permian crinoids are represented as Middle Permian and none are shown in Upper Permian, probably the Middle Permian of the diagrams accompanying this paper should be termed Upper Permian. A two-fold division of the Permian succession in the world is favored, and the rich Timor crinoid collections from Basleo, Bitauni, and Amarassi belong in the lower part of the Upper Permian series, thus defined.

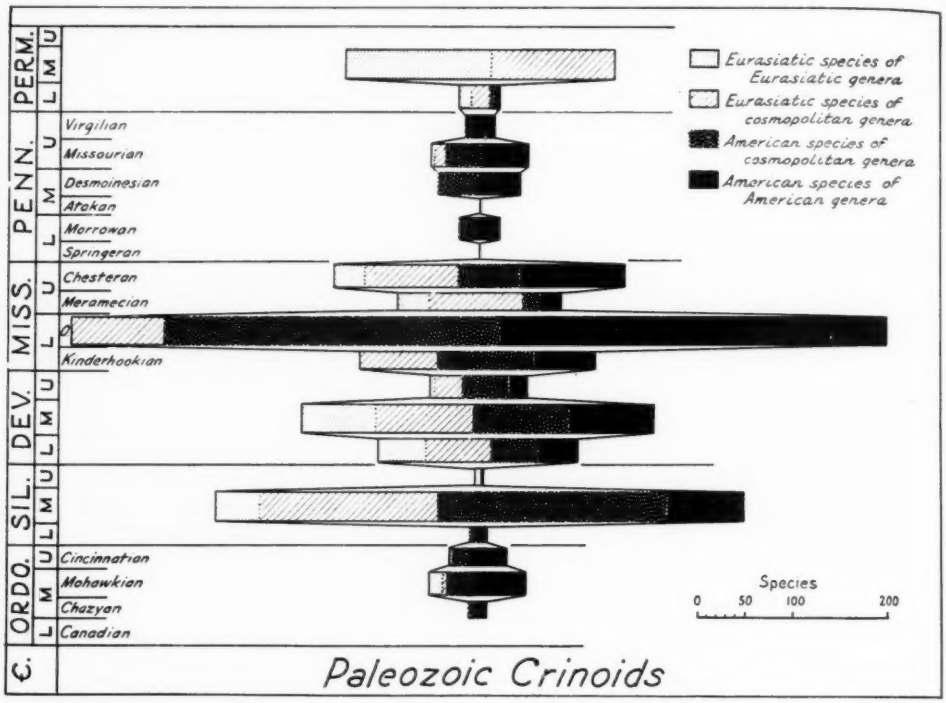

FIG. 1—Distribution of Paleozoic crinoid species, showing classification according to geographic occurrence and assignment to genera having restricted or cosmopolitan occurrence as now known.

INADUNATE CRINOIDS

Inadunate crinoids are characterized by plates of the calyx joined firmly together, with mouth concealed by the tegmen and the dorsal cup lacking interray plates except on the posterior side; the arms are free above the radials. This division, defined as a subclass, includes the orders Disparida, Hybocrinida, and Cladida. Diagrams pre-

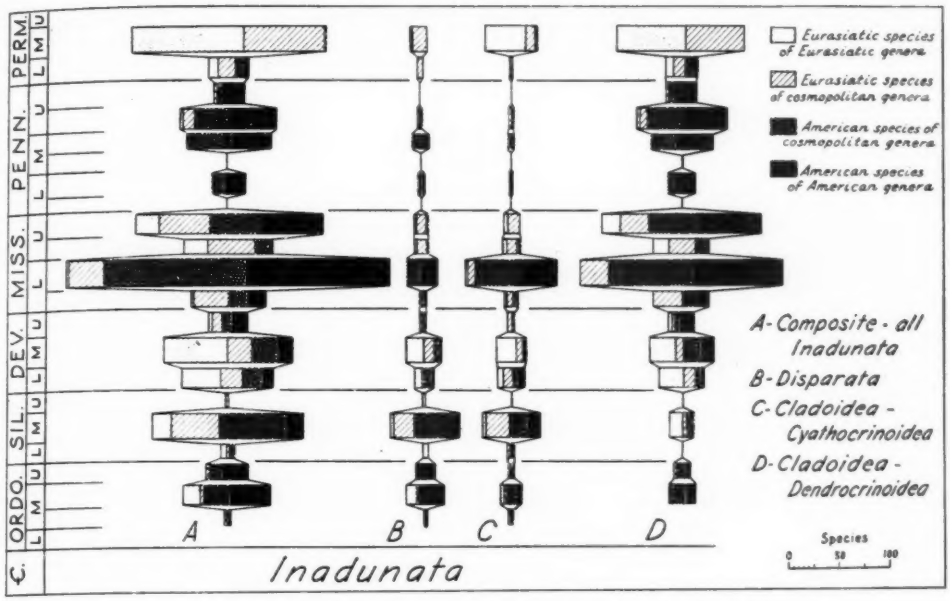

FIG. 2—Distribution of inadunate crinoid species, classified as in Figure 1.

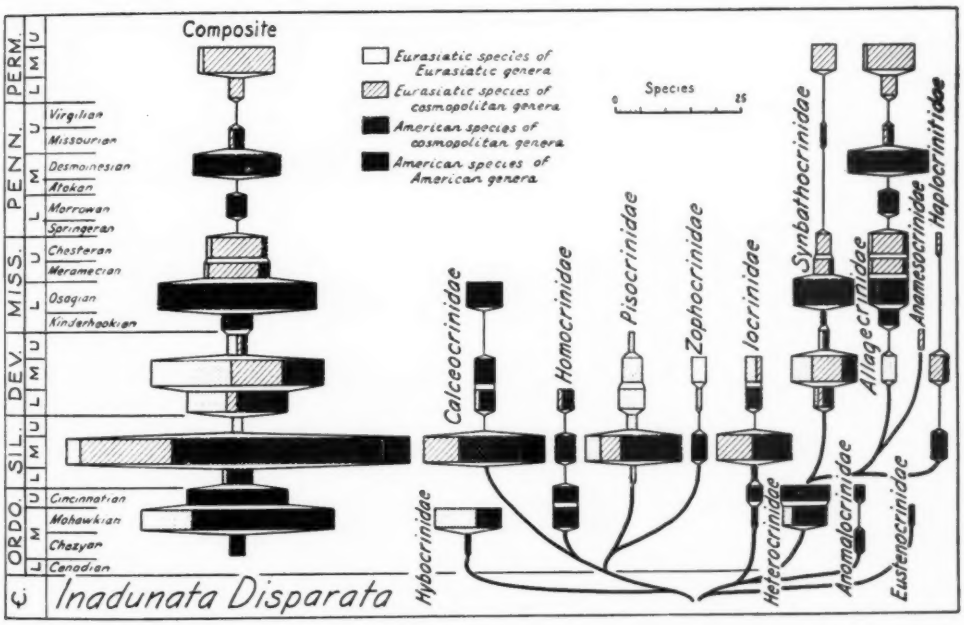

FIG. 3—Distribution of disparate inadunate crinoid species, classified as in Figure 1, with representation of individual families and their inferred phylogeny. The small group of hybocrinids is now judged to constitute a separate ordinal division, correlative in rank with the disparates.

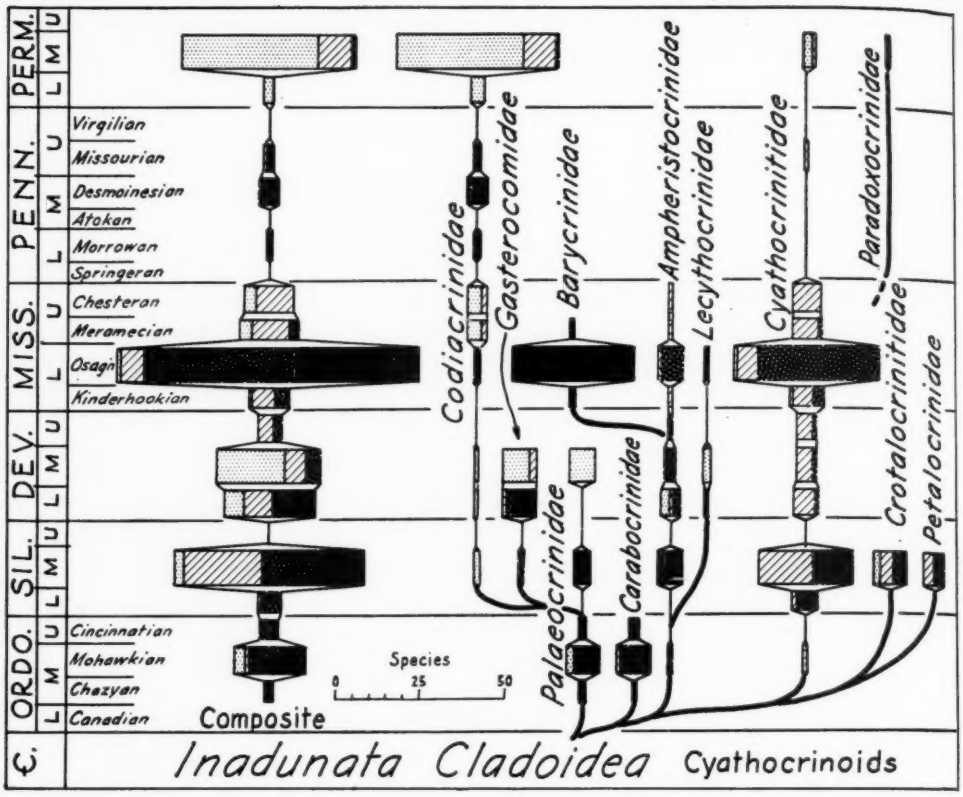

FIG. 4—Distribution of cladid inadunate species belonging to the suborder Cyathocrinina, classified as in Figure 1, with representation of individual families and their inferred phylogeny.

pared for the 1949 symposium at El Paso (figs. 2–5) differ somewhat in nomenclature of taxonomic units from classification now recognized, for Disparata of the figures includes Diparida and Hybocrinida, and Cladoidea of the figures is equivalent to Cladida, now divided in subordinal units termed Cyathocrinina ("cyathocrinoids"), Dendrocrinina, and Poteriocrinina.

The stratigraphic distribution of inadunate species is summarized in figure 2. This shows that maximum development of the subclass occurred in Misisssippian time; subordinate peaks are indicated in Middle Ordovician, Middle Silurian, Middle Devonian, lower Upper Pennsylvanian, and Middle Permian (lower Upper Permian) time. All main divisions of the inadunates range from Middle Ordovician to the Permian, but the disparid and hybocrinid stocks have earlier peak development than others; most prominent in late Paleozoic rocks are representatives of the Dendrocrinina and Poteriocrinina (fig. 2).

Disparida and Hybocrinida.—A composite picture of the disparid and hybocrinid stocks of inadunates is given in figure 3. Beginning in Chazyan, an expansion which is second only to the peak of Middle Silurian time appears in the Mohawkian, and a majority of known species is pre-Mississippian. Eurasiatic representatives are relatively important only in the Devonian, Upper Mississippian, and Permian.

Analysis of species distribution by families brings out the important point that different branches have dissimilar placement. The Hybocrinida are exclusively Middle Ordovician (fig. 3). Among families of the Disparida, three are restricted to the Ordovician and three have peak development in Middle Silurian time. Only two families range higher than Mississippian and of these, the Allagecrinidae are alone

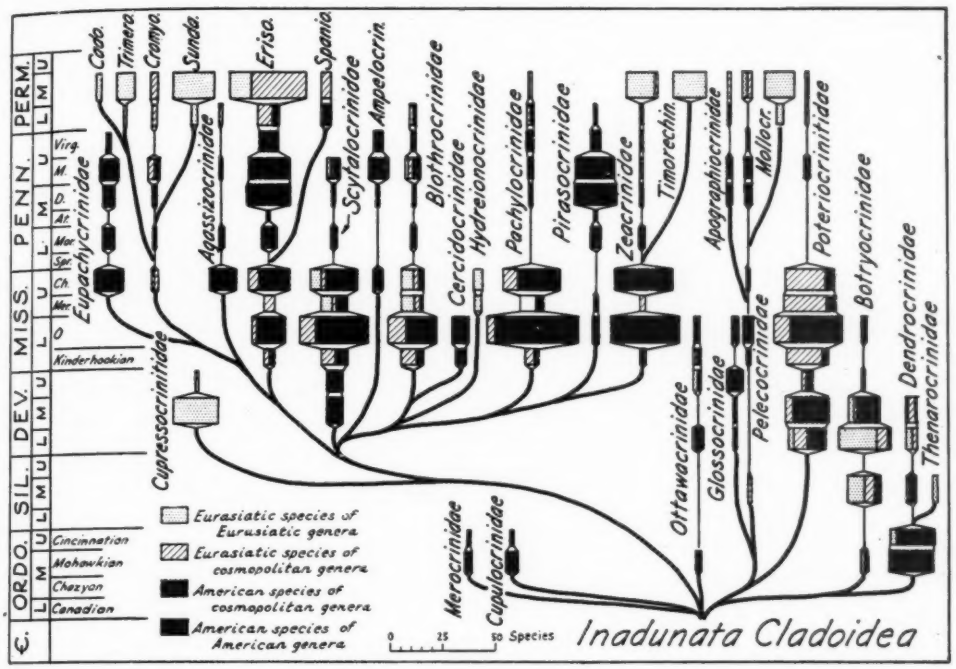

FIG. 5—Distribution of cladid inadunate species belonging to the suborders Poteriocrinina and Dendrocrinina (not differentiated on the diagram), classified as in Figure 1, with representation of individual families and their inferred phylogeny.

important; they include the strangely specialized catillocrinid line represented by several Mississippian, Pennsylvanian, and Permian genera.

Cladida.—The cladid inadunates differ from others in dicyclic structure of the dorsal cup; plates of the posterior interradius indicate genetic affinities with disparids but evolutionary division antedates beginning of the fossil record. The suborder Cyathocrinina is characterized by the bowl-shaped to globose form of the dorsal cup, narrowly rounded radial facets, and lack of pinnules attached to the arms. Geologic distribution of this group is shown in figure 4. Although culmination is indicated in the Lower Mississippian and many species are recorded from the Permian, the cyathocrinine branch of the cladids is a primitive stock, prominent in the older Paleozoic parts of the column. Classification of species by families shows that five of these groups are exclusively Devonian and older, and that prominence of the suborder in Mississippian and Permian assemblages is mainly due to expansion of Barycrinidae and Cyathocrinitidae in the Mississippian and Codiacrinidae in the Permian (fig. 4).

The Dendrocrinina and Poteriocrinina are graphically shown in figure 5. They are distinguished mainly by nonpinnulate arms in the first, and pinnulate arms in the second. The nonpinnulate group is almost wholly restricted to pre-Mississippian formations, whereas pinnulate species are very abundant in Mississippian and later Paleozoic rocks. Most families of the Poteriocrinina range from Lower Mississippian to the Permian.

FLEXIBLE CRINOIDS

The dorsal cup of crinoids belonging to the subclass Flexibilia normally is composed of lower brachial plates, in addition to radials and lower circlets, and these plates are mostly not united rigidly; the tegmen is flexible and arms are uniserial, nonpinnulate. This distinctive group of crinoids was separated from others before the oldest crinoids make appearance in the fossil record, as shown by occurrence of a small number of typical flexibles in Middle

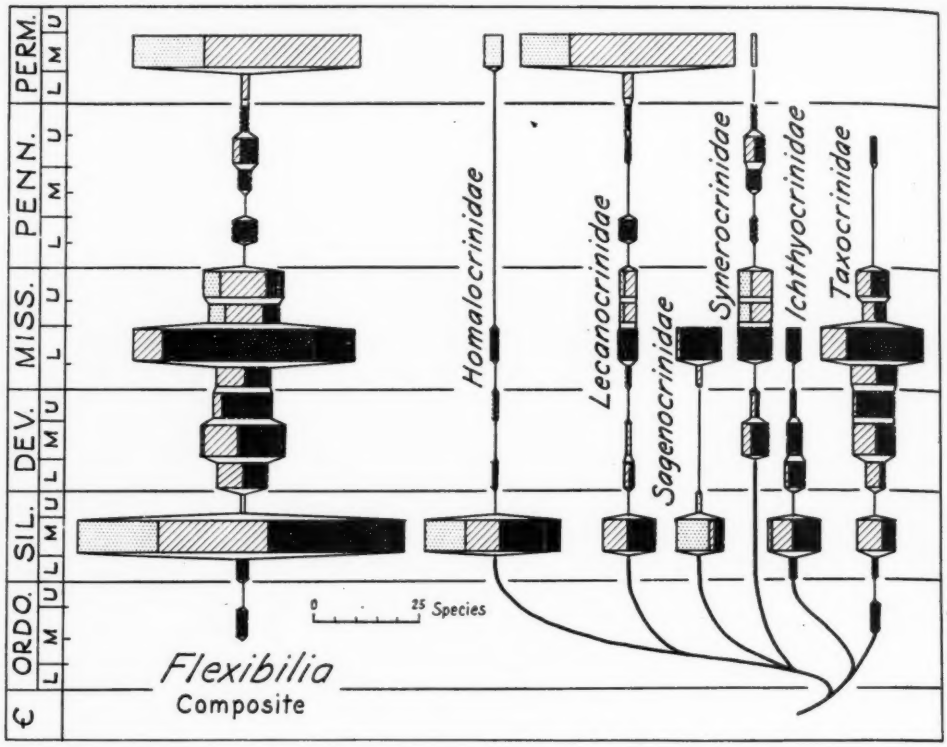

FIG. 6—Distribution of flexible crinoid species, classified as in Figure 1, with representation of individual families and their inferred phylogeny.

Ordovician rocks, associated with camerates and inadunates. Geologic distribution of the subclass is indicated in figure 6. The composite diagram of species shows greatest expansion in the Middle Silurian, and almost as large increase in Lower Mississippian and Permian. The plotted distribution of species by families does not reveal division into groups of families having restricted early Paleozoic development and late Paleozoic development. Rather, all family units seem to be long-ranging, although they differ somewhat in placement of their expansions. The flexible crinoids are a very stable group.

CAMERATE CRINOIDS

Especially characteristic of Paleozoic rocks are camerate crinoids. In this subclass, all calyx plates are united rigidly, the mouth and food grooves being concealed beneath a tegmen composed of firmly joined plates; the dorsal cup includes brachials and generally interradials. A composite diagram of camerate species is given in figure 7. This shows beginning but very modest development in the Ordovician, great expansion in the Middle Silurian, still larger spread in the combined Lower, Middle, and Upper Devonian, and amazing abundance in the Mississippian. Pennsylvanian camerates are almost unknown, but a small splurge is noted in the Permian of Timor. The camerate crinoids are represented by considerably more American species than Eurasiatic, but predominance is attributable chiefly to the abundance of Lower Mississippian species in North America.

Diplobathrida.—The order of camerate crinoids called Diplobathrida ("Diplobathra" in figs. 8 and 10) is distinguished by presence of two circlets of plates below the radials in the dorsal cup. This group comprises a minority of the Camerata which shows less evolutionary divergence and seems generally to have more archaic characters than the single-basal-circlet cam-

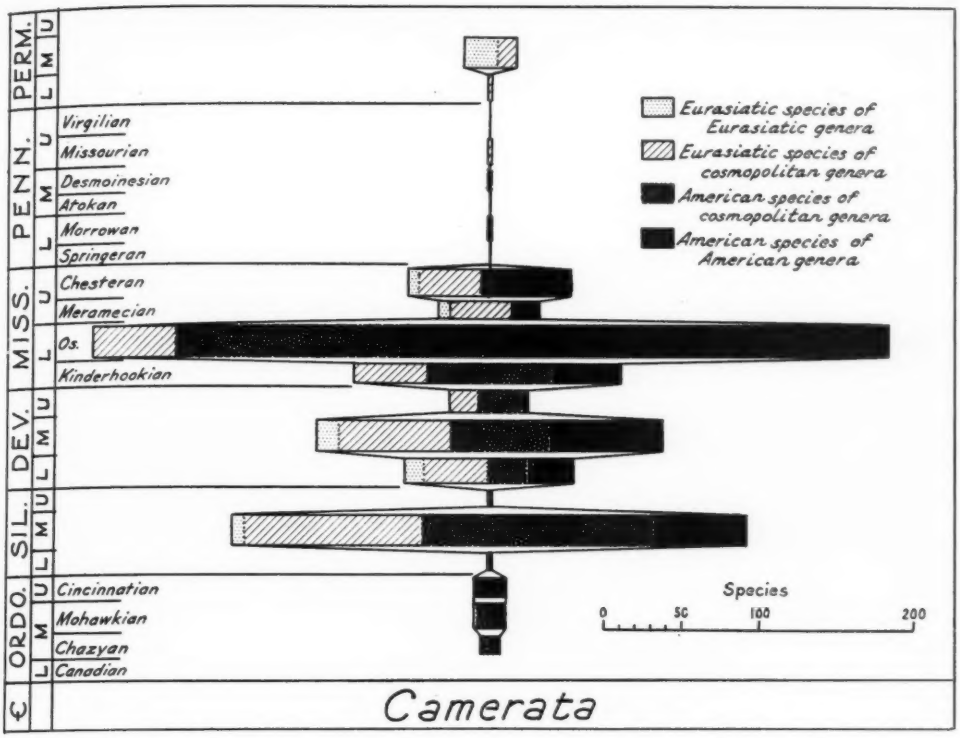

FIG. 7—Distribution of camerate crinoid species, classified as in Figure 1.

erates called Monobathrida. Both orders make appearance in the Chazyan, but the Diplobathrida are more numerous and they have chief development in pre-Mississippian geologic time (fig. 8). Except in the Lower Devonian and Upper Mississippian. diplobathrids are predominantly American crinoids. The peak of Diplobathrida development, represented by number of species, is in the Middle Silurian; approximately 90 per cent of the known forms from these rocks are American.

Distribution of diplobathrid crinoids, plotted by families, shows that only one family unit (Rhodocrinitidae) has any considerable development after Silurian time; other families are exclusively Ordovician, Silurian, or have unimportant remnants persisting into the Devonian. Characteristic Silurian family assemblages are the Dimorocrinitidae, Lampterocrinidae, and Gazacrinidae (fig. 8). The Silurian genus *Nyctocrinus*, which has nearly perfect pentameral symmetry and lacks interradial plates in the dorsal cup, is judged to mark culmination of evolutionary trends in the order.

Monobathrida.—The dorsal cup of Monobathrida ("Monobathra" in figs. 8–11) has only one circlet of plates below the radials. The order contains two suborders named Tanaocrinina and Glyptocrinina, both ranging from Ordovician to Permian but having somewhat different abundance from system to system (fig. 9).

The Tanaocrinina are characterized by a basal circlet of hexagonal outline composed of three equal plates, and by radials separated from lateral contact at the posterior side of the cup by intercalation of an extra plate called tergal. Families belonging to this division of the Monobathrida are shown in figure 10. The most important older Paleozoic groups are the Periechocrinitidae and Desmidocrinidae, but the divergent Barrandeocrinidae, restricted to Middle Silurian, are among the most remarkable of all crinoids in nature of their evolutionary specialization. Chief expansion of the tanaocrinine families is in the Mississippian,

where the families Batocrinidae and Actinocrinitidae are especially abundant; these are chiefly American in distribution. The almost wholly Eurasiatic assemblage of the Hexacrinitidae, confined to the Devonian, is undoubtedly the stock from which the numerous species of Dichocrinidae, mainly developed in Mississippian rocks of North America, were derived. Aside from a few Pennsylvanian species and remnants of four families in Permian rocks, the record of the Tanaocrinina terminates with dying out of the 500 or more Mississippian species.

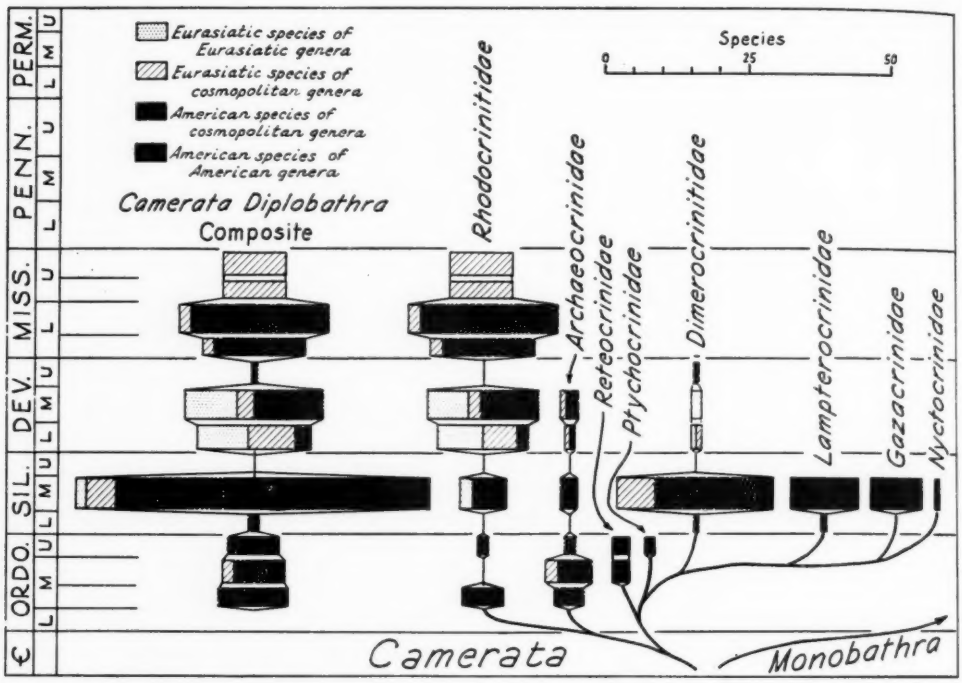

FIG. 8—Distribution of diplobathrid camerate crinoid species, classified as in Figure 1, with representation of individual families and their inferred phylogeny.

The Glyptocrinina have a pentagonal basal circlet typically composed of two large plates and a small one, and the radials are laterally in contact with one another all around. This division of the Monobathrida is represented by Middle and Upper Ordovician species of the Glyptocrinidae, but otherwise it is mainly a Silurian, Devonian, and Mississippian assemblage (fig. 11). Six families are prominent in the Silurian (Patelliocrinidae, Clonocrinidae, Marsupiocrinidae, Eucalyptocrinitidae, Thallocrinidae and Melocrinitidae) and of these six families the first four are entirely or almost entirely restricted to this system. Species belonging to cosmopolitan genera greatly predominate and species from one hemisphere approximately equal those from the other. The main development of the Melocrinitidae is in the Devonian and the important group of the Dolatocrinidae is restricted to Devonian; the former is largely cosmopolitan and almost equally divided between Eurasiatic and American species, but the latter is essentially American in its entirety. The largest single family division of the Tanaocrinina and one of the most distinctive consists of the Platycrinitidae, which has very great abundance in the Mississippian and a long-delayed final burst in the Permian (fig. 11). The Mississippian species of this family belong almost wholly to cosmopolitan genera and are mainly American, but the Permian forms are dominantly Eurasiatic species of Eurasiatic genera; in Permian rocks of Timor, indi-

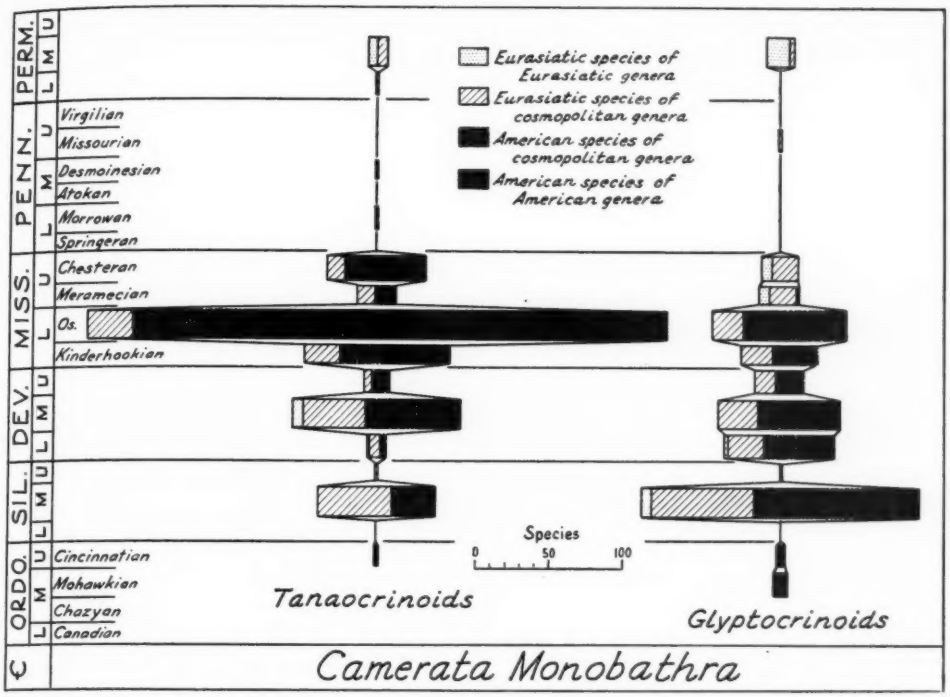

FIG. 9—Distribution of monobathrid camerate crinoid species, summarized by subordinal divisions (Tanaocrinina, Glyptocrinina), classified as in Figure 1.

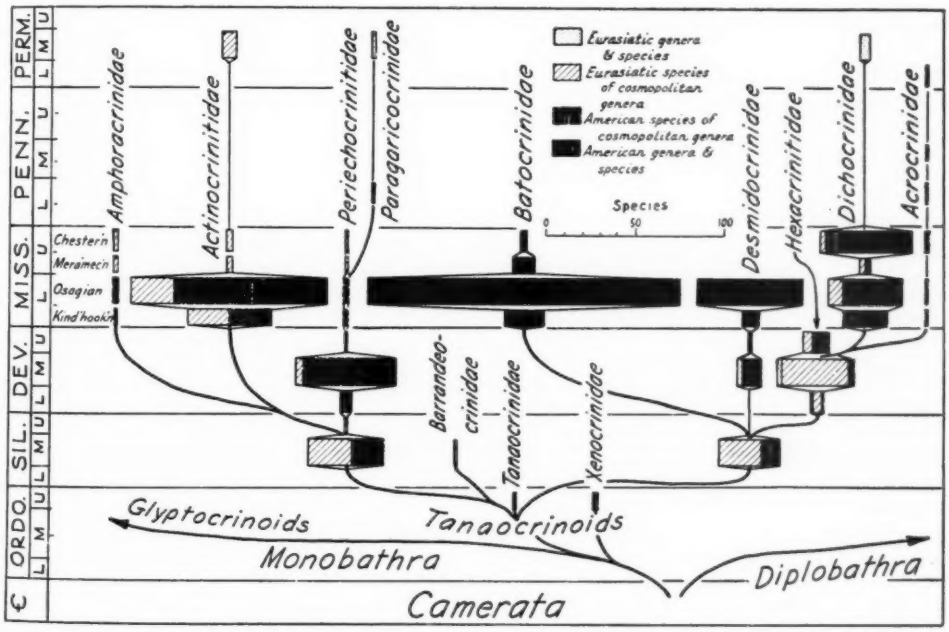

FIG. 10—Distribution of monobathrid camerate crinoid species belonging to the suborder Tanaocrinina, classified as in Figure 1, with representation of individual families and their inferred phylogeny.

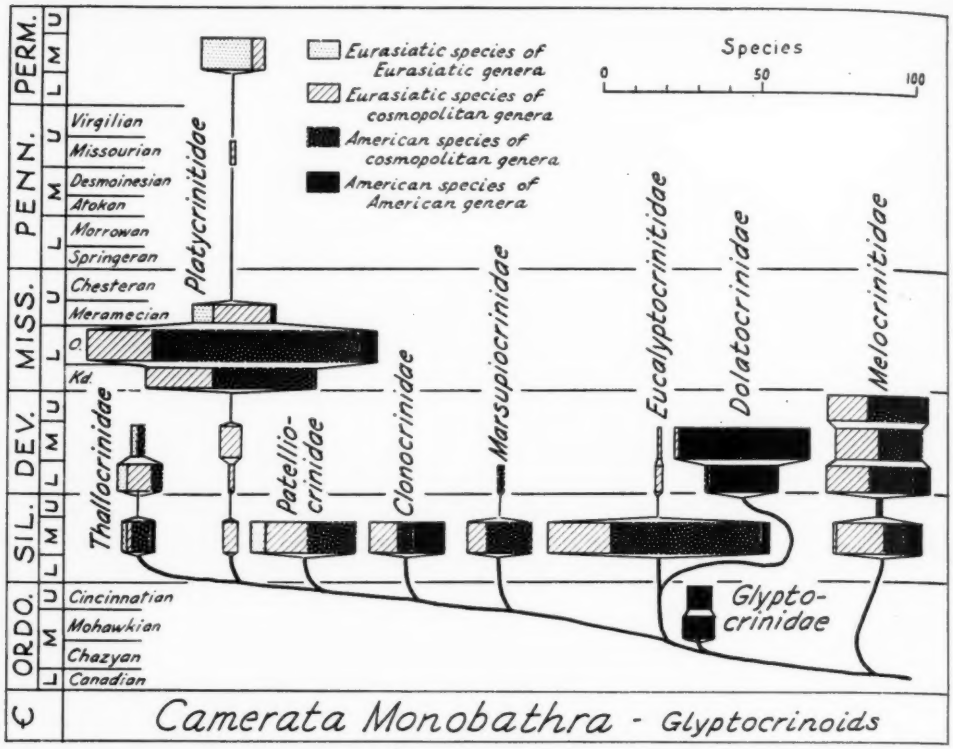

FIG. *11*—Distribution of monobathrid camerate crinoid species belonging to the suborder Glyptocrinina, classified as in Figure 1, with representation of individual families and their inferred phylogeny.

viduals representing some of these species are extraordinarily numerous.

ARTICULATE CRINOIDS

The subclass Articulata contains Lower Triassic to Recent crinoids having a greatly reduced dorsal cup in which the lower (infrabasal) circlet of two belonging below the radials tends to be much reduced or atrophied; the flexible tegmen bears the mouth and exposed food grooves; and the arms are typically uniserial (rarely biserial) and pinnulate throughout. Although evidence exists supporting the view that some articulates may be descendants of flexible crinoids, ancestry of most seems rather clearly to belong in the Inadunata. The articulates may be polyphyletic. As in other divisions of invertebrates, the Paleozoic-Mesozoic boundary coincides with a profound change in the nature of crinoids. The Triassic *Encrinus*, which superficially most resembles some late Paleozoic inadunates, is now classed among Articulata. A composite picture of the distribution of articulate crinoid species is given in figure 12. This shows a "pin-point" beginning of the record in Lower Triassic, modest expansion in Middle Triassic, great development in the Jurassic and Cretaceous, and intermittent small swelling in the Cenozoic, The diagram is misleading in so far as near-disappearance in the Pleistocene series indicates virtual extinction, because the scarcity of Pleistocene fossil crinoids does not parallel the known existence of hundreds of living species. These living species are not included in the figure.

Contrast between distribution of described crinoid species shown in the diagram of articulate crinoids (fig. 12) and that indicated in figures showing Paleozoic crinoids is evident. The known post-Paleozoic fossil crinoids are so predominantly Eurasiatic that quotas from the Western Hemisphere seem insignificant. Only in the

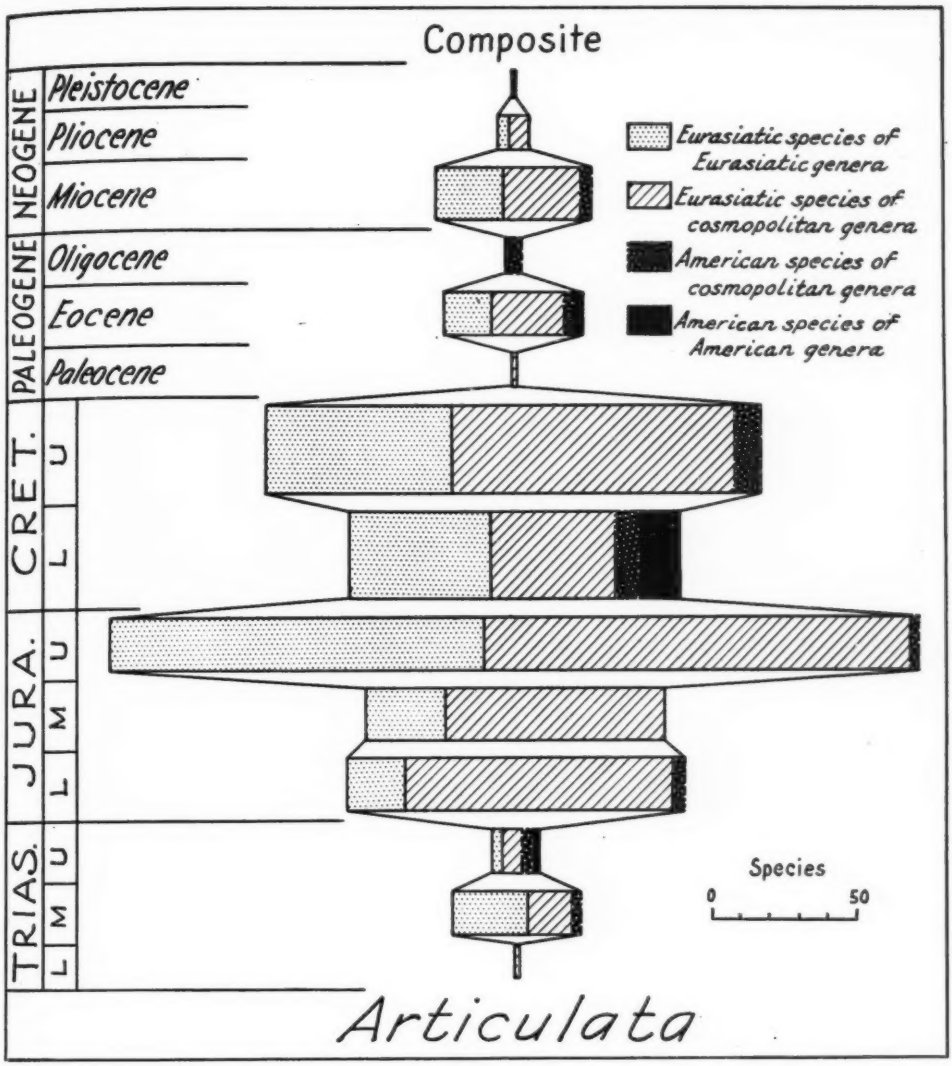

FIG. *12*—Distribution of articulate crinoid species, classified as in Figure 1.

Cretaceous, especially Lower Cretaceous, are American species more than a handful, yet in nearly all other parts of the column, species belonging to cosmopolitan genera predominate. The largest number of species above the Paleozoic is found in the Upper Jurassic.

Family divisions of the Articulata are plotted in figure 13, and this indicates relative prominence of stem-bearing crinoids as compared with stemless types. The free-swimmers comprise the five groups at right side of the diagram, beginning with Marsupitiaide and Uintacrinidae; others are attached crinoids. The dominant Jurassic groups are the Eugeniacrinidae, Plicatocrinidae, Apiocrinitidae, and Pentacrinitidae, all of which are stem-bearing, but the Upper Jurassic contains important representation of free-swimming crinoids in the Comasteridae and Solanocrinidae. In the Cretaceous, the balance definitely moves toward stemless types, but not enough to put them in majority. The trend in crinoids from the post-Mesozoic rock divisions is toward dominance of comatulids.

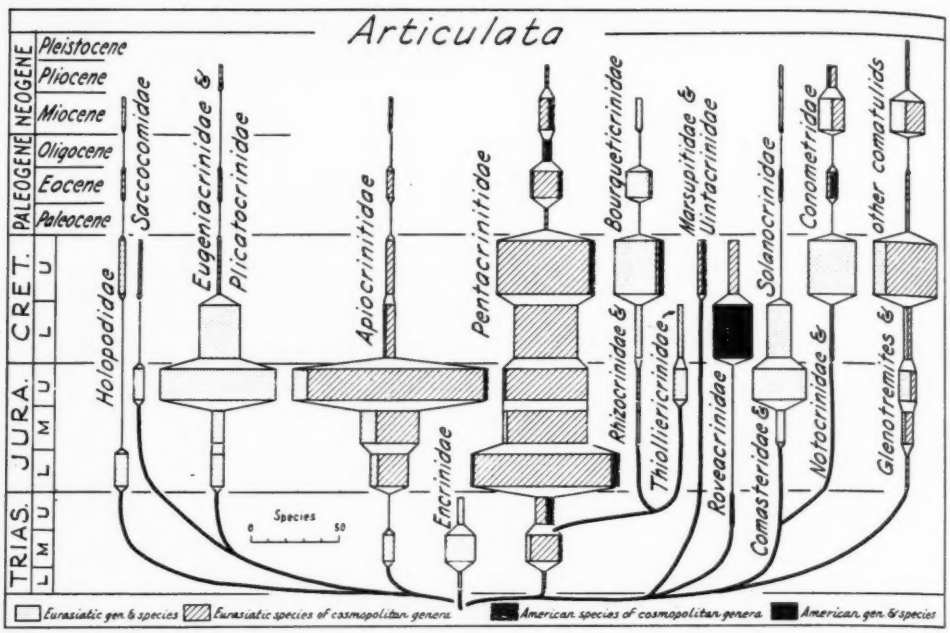

FIG. *13*—Distribution of articulate crinoid species, classified as in Figure 1, with representation of individual families and their inferred phylogeny.

CONCLUSIONS

A survey of all the data on distribution of crinoid species, classified by family, suborder, order, and subclass divisions, and arranged with respect to geographic occurrence, calls attention to stratigraphic and regional concentrations which seem to signify an acceleration of specific differentiation that is more or less localized in time and space. Between these expansions are restrictions. The noteworthy tendency for maximum proliferation of species in middle divisions of geologic systems, generally coinciding with maximum spread of shallow seas over continental areas, is judged not to be fortuitous, because these widespread shallow seas presumably offered best conditions for play of factors stimulating evolutionary differentiation. The fact that different groups of crinoids show response to such conditions in different degrees and at different times may be adduced as evidence that the spasmodic, pulsatory increase and decrease in the census of species reflect real variations in evolution rate between wide extremes. The statement of this conclusion is made without overlooking the point that facies of sedimentation, accidents of discovery, and various other factors which have been mentioned may enter appreciably to obscure and color testimony derived from analysis of species distribution.

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GEOLOGICAL BOUNDARIES IN RELATION TO FAUNAL CHANGES AND DIASTROPHISM

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ABSTRACT—Faunal succession may involve (1) extinction, (2) supplantation plus extinction or suppression of the earlier forms, (3) addition of new elements without extinction or suppression of older groups.

(1) Simple extinction must be due to many causes usually so complex as to be incomprehensible. It is certain that extinctions in one area are not always synchronous with those in another. (2) Extinction plus supplantation by newly developed groups with similar habits, habitats, and often with similar bodily forms, presumably occur more or less simultaneously (in respect to geologic time), and may therefore be more valuable in correlation and the fixing of time boundaries. (3) Addition of new highly successful elements in a fauna may also be a rapidly spreading phenomenon, and consequently of value.

New elements usually appear in the record as migrants from an unknown geographic center. There is no way to determine whether or not they have arisen in an area of intense diastrophism. When they appear they may already be accompanied by new complementary elements (*i.e.*, herbivores plus highly developed carnivores); which makes it probable that we seldom see even the approximate time of original appearance of a group.

This leaves the possibility—indeed the probability—that many of the new faunas have arisen in the regions like many parts of the Southern Hemisphere, which were not affected by the diastrophic changes of the North. When these changes came, certain forms already developed were ready to enter the new habitats and were not necessarily developed by the changed conditions.

INTRODUCTION

A CLOSE inspection of methods available for geologic dating and correlation will surely disclose certain faults and pitfalls. Generalizations based on scattered and scanty faunas, on speculations as to climatic changes, the supposed synchrony and extent of so-called major periods of diastrophism, on the time element involved in the spread of faunas to remote regions, on the unsolved mysteries of so-called universal extinctions, and on the varying rates of evolution in different groups of organisms or in the same groups at different intervals, all form a network of interlacing threads of evidence, much of which may be of such uncertain validity as to leave flaws in the fabric of evidence. Scientific statements based upon uncertainties are useful only if these uncertainties can be counterbalanced by enough facts to form a reasonable probability.

Stratigraphic problems are becoming more and more intricate as data accumulate. In paleontology, the European faunas used by Lyell to subdivide the Tertiary by percentage of extinction would not suffice today to delimit the many subdivisions of that epoch. But the method is still in use. Constant readjustments are necessary in the attempt to bring new knowledge into harmony with old systems—witness for instance the much debated Plio-Pleistocene boundary and the questionable Mio-Pliocene boundaries. What has happened to the Neocene, and the Psychozoic, to say nothing of Dana's "Canadian," and Ulrich's "Ozarkian"? How many proposals have been made for reclassification of the Pre-Cambrian?

Nothing much can happen to our facts, but fitting these facts together to erect well-founded systems of biological classification and geological age-dating is an unending struggle and a likely source of misinformation and confusion. Awaiting possible refinements in absolute age-dating, we are often constrained to fit the facts together in the most probable way, and let the devil take the age boundaries of the geological time scale—the facts and the boundaries don't always coincide.

EXTINCTION OF REPTILES AND THE MESOZOIC-CENOZOIC BOUNDARY

Let us examine a few samples of our facts and methods, in relation to vertebrate faunas, and so-called boundaries. One of the great events in the vertebrate record is the extinction of several groups of large reptiles and their replacement by small mammals all over the world. We have been told that this event took place at the end of the Cretaceous, that it was a remarkably sudden extinction, and that the mammals blossomed out rapidly or explosively following their release from competition with the reptile hords. This may not be an exact formulation of the views of some of my colleagues, but it seems to be a generally accepted idea.

Just what do we have in the way of evidence? We know that mammals of a sort lived alongside the reptiles for about 100 million years without becoming larger than modern beavers and without attaining any great diversity of form. We know that none of the modern types of mammals except the marsupials and insectivores are to be found in the fossil record until after the great extinction of the reptiles. And even then the modern orders came in over a long period of some 25–30 million years, hardly an explosion. We know that mosasaurs, plesiosaurs, dinosaurs and pterodactyls are found together until their last appearance. Ichthyosaurs disappear a little earlier and eosuchians (champsosaurs) a little later. We know that crocodilians, insular rhynchocephalians, turtles, lizards and snakes lived right on through the great extinction and were apparently not affected by it. We know that birds, fishes and flowering plants were not greatly affected. We know that ammonites and belemnites are not found with the very last mosasaurs, so they probably became extinct before the final disappearance of these sea-going lizards.

We therefore conclude that the period of extinction was a long one in the possible range of 20–30 million years, so we cannot be certain that the extinction of any of the reptiles was simultaneous in a world sense, and we may presume that it was not simultaneous except in a very rough geological sense.

The great danger in this problem is an obvious fallacy—we call the period of great extinction the end of the Cretaceous, we assume that many of the extinctions were world-wide and simultaneous, and therefore when we find dinosaurs, we automatically place them in the pre-Tertiary. Then we are prone to proceed a step farther to postulate some universal diastrophic or catastrophic event and/or change of climate to account for the extinctions.

We may reasonably question the general idea of world-wide diastrophism and in particular, world-wide Laramide diastrophism. There seems to be no great break between the marine Cretaceous and Tertiary of California and no evidence of any great diastrophism along the West Coast between the Upper Jurassic and the late Tertiary. Nevertheless mosasaurs, plesiosaurs and dinosaurs occur together and for the last time in the Moreno formation, which is placed in the Upper Cretaceous. The exact upper limit of the California Cretaceous is, of course, in dispute. It would be very tempting to place it at the top of the Moreno where the last mosasaur has been found, because in Europe the last mosasaurs are found in a phase of the Danian in which ammonites and belemnites do not occur. Then one might go into the Southern Hemisphere and delimit the Cretaceous by the same procedure. But one could wish to be more confident about the synchrony of these boundaries. They might even be called fanciful in the Southern Hemisphere, where organisms have a way of surviving much longer than they do in the north.

Can we possibly find support for the suggestion that the great reptiles were exterminated by extreme climatic changes? One recent view is that heat caused the large reptiles to die out because it has been shown experimentally that heat affects spermatogenesis and causes sterility in modern reptiles. Birds and mammals, fortunately, have means of preventing overheating of the gonads. This has led to the hypothesis that the end of the Cretaceous must have been a torrid period over the earth and across the seas. One of the objections to this idea is that sea-living reptiles as well as those confined to inland waterways were exterminated along with the land dinosaurs and pterodactyls. Marine tempera-

tures then must have risen to lethal levels. This is unlikely and is not supported by H. C. Urey's (1950, pp. 462–463) recent determinations of marine temperatures in the Cretaceous seaways of North America. His carbon isotope thermometer gives temperatures of from about 18–20° C. at the beginning and end of the Cretaceous and 26° C. at mid-Cretaceous. Then, too, the northern distribution of plants would imply that there was no prolonged or severe cooling at the end of the Cretaceous.

This leaves us with another possibility, yet to be more fully demonstrated, that the great sluggish reptiles were in some way, or in many ways, supplanted by the small active mammals of the Paleocene; not a wholly satisfactory conclusion.

One might suppose that ichthyosaurs, piesiosaurs and mosasaurs were supplanted by zeuglodont whales and that dinosaurs were replaced by land mammals; but so far as present evidence goes, there were large time gaps between the extinction of the reptiles and the appearance of probable mammal competitors.

As usual, we must lean upon an unknown combination of factors, which is a fancy way of saying we just don't know.

We face much difficulty in applying the standard geological time scale to the Southern Hemisphere. Perhaps we have enough to do in the North without worrying about the South. But here is a case in point.

Thecodont reptiles including the pseudosuchian ancestors of dinosaurs, birds, pterodactyls and crocodilians, are confined conventionally to the Triassic. The pseudosuchians appear abundantly in the North American Moenkopi formation and the European early Triassic and disappear along with the phytosaurs, therapsid dicynodonts and the last of the stegocephalians at the conventional Upper Triassic boundary. This boundary, however, is in dispute, as most boundaries are, even in places where it should be most clear. In the southwestern United States, a continuous record of continental sedimentation apparently crosses this alleged boundary at all time levels when such a boundary could conceivably exist. The upper beds of the Chinle formation in northern Arizona are mostly red mudstones interspersed with layers of marly, shallow-lake limestone beds which are fairly separable from an overlying series of brownish-pink, partially eolian beds called the "orange-red sandstone." The "orange-red sandstone" in or on the Chinle beds in turn supports the partly fluviatile Wingate sandstone in this region. Above the Wingate over wide areas lie the eolian beds of the Navajo sandstone which are interspersed with thin fresh-water lime and gypsum beds topped by sediments that lie below and within the swamp beds of the Morrison formation which in turn must be close to the Lower Cretaceous boundary because it has been placed in both the Upper Jurassic and Lower Cretaceous in previous disputes.

In South Africa there is a similar sequence of rocks containing comparable vertebrate elements. In Africa advanced capitosaurian and cyclotosaurian stegocephalian amphibians occur with abundant and varied mammal-like reptiles in the so-called Middle Triassic, *Cynognathus*-redbed zone of the Karroo and go no higher. The Molteno formation, next above, contains a flora of alleged Upper Triassic age and is surmounted by a series of dinosaur- and crocodile-bearing redbed mudstones capped by massive eolian sandstones—the Cave sandstones.

Now these dinosaur-crocodile beds at the top of the Karroo series in South Africa are usually placed in the Upper Triassic. The North American "orange-red sandstone" beds above the Chinle formation, with comparable dinosaurs and crocodiles have also been regarded as Upper Triassic. But crocodiles are not known in Europe until the Lower Jurassic and dinosaurs are not highly advanced in Europe and North America until that time. Also in Europe the stegocephalians become extinct at the end of the Triassic and are never associated with crocodilians.

If we accept this evidence uncritically, we should place the upper limit of the Triassic in Arizona between the upper part of the Chinle and the "orange-red," at the time of the disappearance of dicynodonts, phytosaurs and amphibians in the Chinle, and before the advent of crocodilians in the "orange-red." To be consistent, we should place the same boundary in South Africa between the Molteno and the Redbeds, after

the time of disappearance of dicynodonts and amphibians, and before the advent of crocodilians and dinosaurs.

This is at least consistent and logical, but not necessarily correct for it implies or assumes: (1) that changes toward desert climate occurred at the same time in the two widely separated regions; (2) that elimination of the mammal-like dicynodonts and stegocephalian amphibians was practically simultaneous in the two regions; (3) that crocodiles replaced primitive thecodonts at the same time in Europe, North America and South Africa; (4) that time boundaries coincide with formational boundaries. This is an almost incredible picture.

Perhaps this is a fair example of how vertebrate specialists work. But I venture to say that no one will immediately alter the South African or North American boundaries because of this evidence. We must await the discovery of some more universal means of getting an absolute time scale. Only then shall we discover how accurate our long range correlations may be.

PLEISTOCENE BOUNDARY PROBLEM OF AFRICA AND NORTH AMERICA

A more easily demonstrated source of error is obvious when we compare the Pleistocene of the Northern Hemisphere—where incidentally both the upper and lower boundaries are in dispute—with the still more vague Pleistocene of South Africa. The Northern period was a time of extinction of large mammals, and the faunas have become impoverished mainly during the last 30,000 years. But in South Africa there was no such widespread extinction. There was apparently a succession of baboon and elephant genera. A sabre cat, a large horse, a giant hyrax, and a few extinct species of living genera of reptiles and mammals existed until a few thousand years ago. The fauna today is essentially a Pleistocene one in northern terms.

If we could imagine man coming on the scene several million years hence, he would very likely synchronize the present day African fauna with the North American Pleistocene, on the vertebrate evidence. Possibly this kind of anachronism has penetrated our evidence in the past.

SUPPLANTATION AS A BASIS OF CORRELATION

Professor Simpson in his periodicity charts has shown that evolutional periodicities do not coincide with diastrophism in anything more than a haphazard way. Every group has its own periodic system. So one suspects that where close coincidences do occur, they may be the result of circular reasoning.

But there are means available to establish some integration between biological periodicity and regional geological events—even though little or no causal connection between the two may be indicated. May we assume that supplantation of one group by another can be used to bolster the evidence afforded by time of origin, periods of expansion and time of extinction? May we further assume that the time of expansion of a group will most likely coincide with the time of extinction of an ecologically antecedent group, and that this time of replacement will be, geologically speaking, simultaneous in interconnected areas? This ecological supplantation may be competitive—due to actual extermination by competition; or non-competitive—due to supplantation without direct competition. It may also be complete or incomplete. Many examples of direct competition may be seen going on today as man eliminates dangerous or competitive mammals from his environment. Such things evidently happened when South America was connected with North America in the mid-Tertiary. Here a relatively weak crustal movement has produced a profound biological upset.

Indirect supplantation may be less easily perceived, less easily deduced from the record. We suspect that some sort of indirect supplantation occurred when dinosaurs were replaced by small mammals. Something exterminated the dinosaurs—it was probably not the small mammals—the small mammals moved in and soon developed large forms, much larger and more diverse than anything in the previous hundred million years or more of Mesozoic mammalian history.

Whatever the cause—whether competitive or non-competitive—supplantation of one group by another furnishes additional

evidence for correlation over any series of interconnected lands or seas. There is no evident reason why such correlations should be forced into coincidence with geological time boundaries—but they may usefully indicate chronographic episodes of regional or even world-wide significance.

POSSIBLE CONNECTIONS BETWEEN GEOLOGICAL EVENTS AND EVOLUTION

Although there seems to be some lack of biological evidence for world-wide simultaneous geological events, we may still recognize the influence of climatic changes often produced by geological events on the course of life. The main question is the coincidence in time of such changes over the earth. We are perhaps more likely to overemphasize the climatic and other physical events and underestimate the interaction of more subtle biological influences.

Thus the mysterious explosion of hard-shelled invertebrates in the Cambrian might be regarded by a geologist as due to some change in the oxygen ion content of sea water—an increase of the oxygen content, which would permit lime salts to be laid down more readily by organisms. Objections to this idea are (1) the presence of lime-forming plants in the pre-Cambrian; (2) the origin of chitin-bearing crustaceans in the Cambrian along with the newly developed lime secreting organisms.

Perhaps a more probable kind of theory would be some sort of biological explanation; such as, (1) that predatory animals of some primitive soft-bodied types may have driven the early Cambrian invertebrates to develop shells, tubes and hard skins, or (2) that invertebrates were not sufficiently well organized to produce hard skeletons in the pre-Cambrian. Whatever the reason, we have taken the phenomenon and put a time boundary below it. Now that we have this line, we may be tempted to connect it with some major geological event. We hope that such an event may prove to have been fairly universal, but was it?

When chordates arose, we judge that they must have been small, active, transparent, non-predaceous forms with ciliated mouths only capable of ingesting small organisms. When vertebrates first appear in the fossil record, they were the great-grandchildren of these earliest forms—which in the late Ordovician gained hard shells and settled down quietly in the mud to continue the diet and manner of feeding of their ancestors.

The earliest fishes of the Silurian found this kind of life too slow, they chased their prey and killed it by seizing it in jaws and teeth—new structures. Predatory fishes developed so rapidly in the Devonian that they scared some of their less able relatives out of the water onto land, or did they? A geologist might say that the Devonian developed periods of aridity when the drying ponds and streams forced some of the fishes to develop feet and walking limbs, to struggle overland toward wetter holes to moisten their desiccated skins and seek their aquatic prey.

We may regard the geological view as the least-likely, for the Devonian, despite its alleged aridity, witnessed one of the grandest expansions the fishes have ever undergone, with prodigious increase of predatory arthrodires, acanthodians, early sharks, dipnoans, and rhipidistians. Some time during the Devonian, the latter lost their gills, changed their fins to feet and became amphibians, the first land crawlers. A period of maximum expansion of predatory fishes then seems to have immediately preceded the origin of the tetrapods which was primarily a biological event, not necessarily connected with a geological change.

During the Carboniferous and Permian, the amphibians experimented with various locomotor mechanisms, particularly improvements in the vertebral column that would permit more active movement on land. After the achievement of a reptilian type of column—which the birds and mammals and modern reptiles still preserve—the reptiles arose from among certain stocks that discovered a way to produce progeny on land in smaller numbers, without the necessity of going through a tadpole stage. This event took place in the late Mississippian or early Pennsylvanian. No profound geological stimulus was evident or likely, but we might note and hold in mind a co-

incidence between the flowering of the stem reptiles in the Permian and the great orogenies of that period.

There are four genera of cotylosaurs in the Pennsylvanian, forty in the Permian, and only nine in the Triassic. Romer lists three genera of pelycosaurs in the Pennsylvanian, one of which continues into the Permian, and thirty-three more in the Permian, with only one doubtful genus in the Lower Triassic. But the question has been raised, were the earliest reptiles Carboniferous upland types which have not been preserved owing to lack of suitable deposits?

The mammal-like therapsids almost completely supplanted their pelycosaur ancestors in the Middle Permian and expand prodigiously in the Upper Permian and Lower Triassic, waning rapidly and barely entering the Lower Jurassic, when they gave rise to the mammals. At that time climatic influences may have been at work—possibly an increase of aridity and seasonal climates colder in winter.

Supplantation of therapsids by diapsid archosaurs was rapid and complete at the close of the Triassic. The last degenerate stegocephalians gave way at the same time, whether forced out by aridity or by competition with advanced reptiles, we cannot say.

The idea of aridity is complemented and supported to some extent by a paucity of Lower Jurassic fishes and sea reptiles, and the rise of lizards. Ichthyosaur genera number thirteen in Middle to Upper Triassic, nine in the Jurassic, and only five in the Cretaceous. Protorosaurs and araeoscelids disappear toward the end of the Triassic and ancestral plesiosaurs undergo their first expansion with 32 Triassic genera, followed by 18 in the Jurassic (10 in the Lower Jurassic) and 24 in the Cretaceous.

Thecodonts (pseudosuchians and phytosaurs), mostly swamp and mud flat dwellers, are confined entirely to the Triassic, where the early ones gave rise to the bipedal ancestors of the dinosaurs, the later ones to the ancestors of crocodiles, pterodactyls and birds. The main flowering of the pterodactyls seems to have occurred from the Upper Jurassic to the Lower Cretaceous—15 genera in the Jurassic and 7 in the Cretaceous, with only three in the Upper Cretaceous where the last giant pterodactyls must have come into active competition with the birds.

The dinosaurs arose in the Middle Triassic (24 Triassic genera), became abundant in the Jurassic (67 genera), and continued to increase in the Cretaceous up to the very end of that period (154 genera). This is the greatest expansion known among the lower tetrapods, and culminated in the most sudden extinction—an extinction involving many diverse types. It has come to be recognized as a key to the marking of the continental Cretaceous upper boundary. The evidence would incline one to accept the general accuracy of this important boundary. But I think we might withhold judgment as to the general biological effect of the Laramide revolution, and view other revolutions as well with great suspicion.

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PERIODICITY IN VERTEBRATE EVOLUTION

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ABSTRACT—Graphs are presented showing rates of known origin ("first appearances per million years") of orders, families, and genera in each of seven classes of vertebrates (omitting birds) for each period of their history from Ordovician to Tertiary. One, two, or three peaks occur in each class when these rates reached a high and after which they declined, usually sharply. Peaks in rate of origin of orders regularly precede those for genera by some 25 to 50 million years. A similar span intervenes between the first appearance of each new major adaptive type or structural grade and the ordinal peak that regularly follows such an event. Altogether, the sequence suggests a cycle in a continuous process. Episodes of "explosive evolution" cannot be defined as limited to or caused at any particular point in the process, and therefore periodic diastrophic episodes in the earth's crust cannot be shown to have a causal relationship to them. Classes and other major groups do not demonstrably tend to arise at or immediately after period boundaries or the tectonic episodes commonly supposed to define these. The real periodicity that does appear in vertebrate history seems to result from orderly evolutionary progression, succession, and replacement rather than being conditioned primarily by any periodic physical phenomena. Physical events in earth history are among the complex factors which, all together, produce and guide evolutionary change. Little support is found, however, for the theory of simultaneous, world-wide physical and biological climaxes at the period and era boundaries.

INTRODUCTION

SEARCH for *the* cause of evolution has been abandoned. It is now clear that evolution has no single or simple cause. Its process is a continuous flux in which the total situation of any instant is the result of all previous changes and the cause of all that follow. This total situation includes the physical environment, all the biological elements of ecological associations, and an intricate complex of genetic, associative, and other factors within each of the evolving population groups. In the broad constellation of conditions determining the course of evolution, changes in physical environment necessarily change the total situation and they are therefore necessarily accompanied or followed by some sort of evolutionary change. This relationship is firmly established and is not here under dispute. The precise nature of the relationship, its effect on the broadest or most basic episodes in evolution, and its possibly periodic recurrence are, however, still in need of discussion.

The main purpose of the present symposium is to determine, first, whether there are periodic, general, essentially world-wide times of intensified evolutionary activity and, second, whether these correspond with similarly general and periodic increases in diastrophism, evolutionary events in the physical history of the earth's crust. The intention is to test a possible causal relationship, existence of which has commonly been taken for granted and is widely taught as fact to students of historical geology. The dogma has, however, been repeatedly questioned both on the biological and on the physical side. The choice of the topic for this symposium shows that doubts exist as to the validity of earlier conclusions on this subject.

This particular contribution is concerned with the biological aspect, only, of the problem and with the evidence of a single phylum of animals, the Vertebrata. The data for this phylum, although obviously incomplete, are exceptionally good both in the abundance of paleontological records and in the progress that has been made in their compilation and interpretation. The present aim is to summarize some of these data in such a way as to bring out any periodicity or other regularities that may exist in episodes of proliferation and of extinction among vertebrates. Discussion will then bear on the possible evolutionary signifi-

cance of such regularities as are found and on their possible correlation with events in earth history.

DATA

The problem involves origins, increases, decreases, and extinctions of groups of vertebrates. The data are records of occurrence of the various taxonomic entities within each period (or, as may be practicable, epoch or age). Strictly speaking, the factual data do not include times of origin or of extinction, but only the times of first

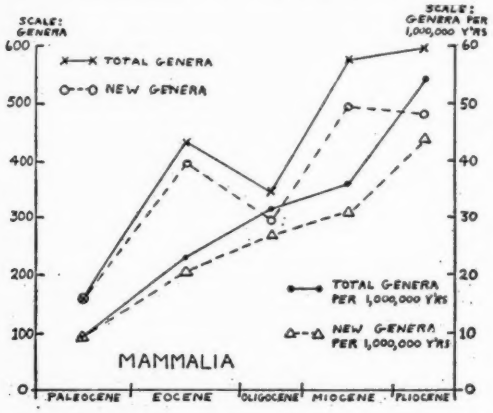

FIG. 1—Graphs of numbers of known genera and of new genera (or first appearances) of mammals in the epochs of the Tertiary.

and last appearance in the record as known. These times of appearance certainly do not correspond precisely with real origins and extinctions, nor can the recorded increases and decreases be taken as accurately proportional to those that really occurred. In the present summary it is unnecessary to to enumerate or evaluate the numerous sources of error, although these have been carefully considered and allowance has been made for them in deductions from the record. The data are taken as they are. First appearances in the known record are accepted as more nearly objective and basic than opinions as to the time when each group really originated.

The record thus compiled is clearly not random, as will appear below. It has a large measure of regularity and consistency that seems to attest correspondence with real events. In particular, well-marked trends of increase or decrease seem, with some exceptions and when taken broadly, to be significant even though they cannot furnish a precise measurement of the real rates. Sharply delimited highs and lows in recorded frequencies seem, with similar exceptions and precautions, to correspond closely with times of real maxima and minima in proliferation of the groups in question.

Data were compiled for the most part from Romer (1945), with some additions and modifications especially as concerns mammals. The basic compilation (assisted by Nathan Altshuler) was made as part of a larger project to survey some numerical aspects of the whole fossil record of animals, jointly with Norman D. Newell and assisted by numerous other specialists. Dr. Newell and I hope to present these data more extensively and to discuss other aspects of them elsewhere. Here such data as seem to bear most closely on this particular problem are summarily presented in the form of graphs, only.

The numerical data consist of a census for various taxonomic categories known for various times in the geological record. Analysis of numbers of species was not attempted because of factors, relating mainly to sampling and to subjectivity, that make inferences from them excessively unreliable. Within the Vertebrata, records of orders and genera are most useful. Records of families have also been compiled and are included in some of the present graphs (figs. 2–3), but in general they add little to what is shown by the orders and genera. For each time and for each selected taxonomic level, figures in the tabulations (not here published as such) include total numbers, first appearances, last appearances, and continuations from preceding times. For the particular subject of this paper, first appearances are most significant because interest is focused mainly on times of maximum proliferation or episodes of so-called "explosive" evolution. It is also true that the total numbers, especially for genera, usually closely follow the general trends for numbers of first appearances, as can be seen in fig. 1. Some broad data on last appearances (fig. 5) and on totals and survivals (fig. 6) are given but emphasis is here on first appearances.

Numbers of known taxonomic units are given by periods and not by shorter time units except for mammals, which are in some graphs (figs. 1, 3) tabulated by epochs in the Tertiary. Some allowance must be made for the fact that the long time-units, least 3 to 1. (Few geologists will question that the Cambrian was three times as long as the Mississippian, for instance, or that the Eocene was about twice as long as the Oligocene.) With a constant rate of proliferation, the graphed values of first appear-

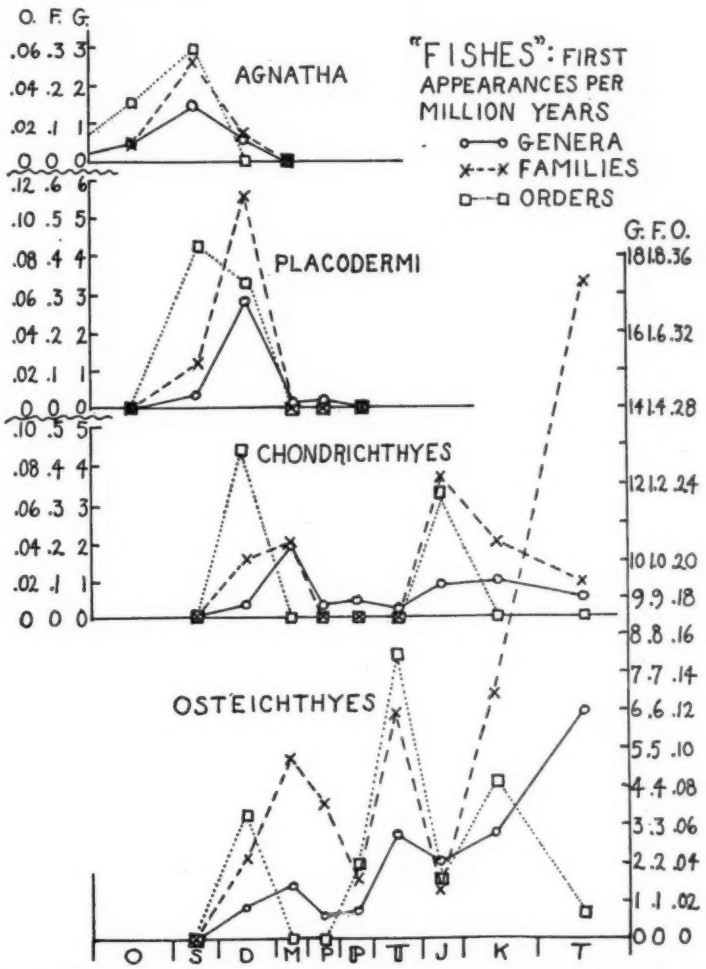

FIG. 2—Graphs of first appearances per million years of known orders, families, and genera of the four classes of "fishes." O., F., and G. above the scales stand for orders, families, and genera per million years. The time scale at the bottom is divided into geological periods, from Ordovician to Tertiary.

although useful for purposes of broad summary, conceal some important details. Similar allowance is necessary for the conventionalization of placing each record at the middle of the corresponding time unit.

Even if the exceedingly short Quaternary period is omitted, the lengths of the geological periods or epochs differ by a factor of at ances would be much higher for a long period than for a short period. The fact that the lengths of the periods are not accurately established introduces another uncertain and subjective element, but comparability is better if allowance is made for variations in these lengths. In most of the graphs (figs. 2–5), this is done by showing, not the

total count for each period, but this count divided by the assumed length of the period in millions of years. This usually does, in fact, produce smoother and apparently more consistent graphs, as shown by the example of fig. 1. The time scale at the bottom of each graph shows the relative assumed lengths of the periods.

tions for those epochs would require lengthy discussion and adjustment of the data.

PEAKS OF RATES OF FIRST APPEARANCES

The curves of first appearances per million years for seven classes of vertebrates (figs. 2–3) show certain characteristics common to all or most of these classes. Each

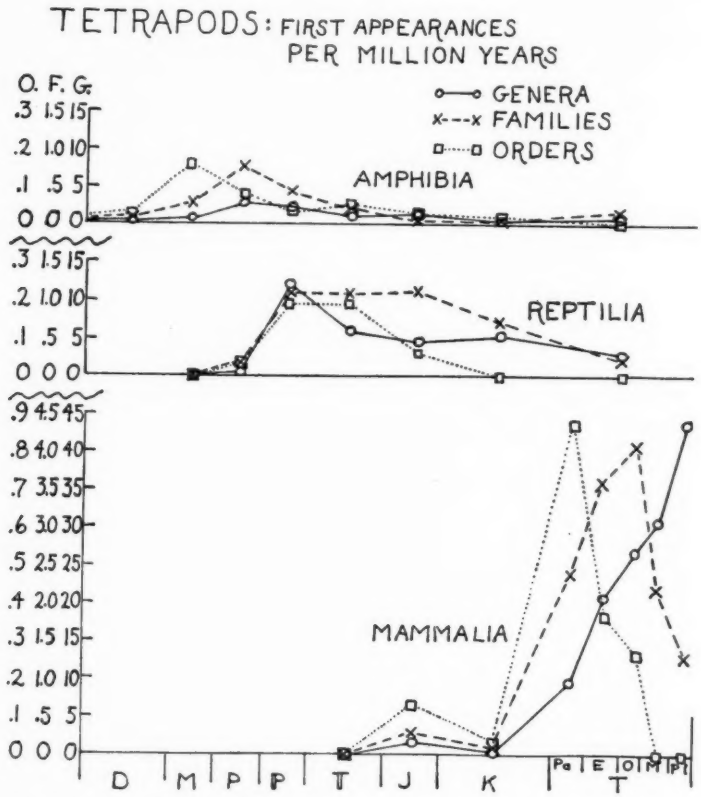

FIG. 3—Graphs of first appearances of three classes of tetrapods. Method of construction and abbreviations as in Fig. 2, with addition of the Tertiary epochs to the time scale for the Mammalia.

The fossil record of the birds, which is still very poor, involves so many adventitious irregularities and would require so much inference and discussion that it is omitted here. Such as it is, this record (which has also been compiled and graphed but not published) is not inconsistent with conclusions drawn from other, better data for vertebrates as a whole. For all the groups, Pleistocene and Recent records are omitted, because the very different sampling condi-

curve, whether for orders, families, or genera, rises to a relatively early peak, generally in the period of first appearance of the class or in the following period. Only for the family and generic curves of the Amphibia is the first peak as late as the second period after that of first appearance of the class. Mesozoic mammals are so poorly known that the reality of the low, recorded Jurassic peaks may be questioned, but better knowledge is more likely to emphasize these peaks

than to eliminate them. Each curve tends to fall off rather rapidly from this first peak. In the period following the peak, there is a significant drop in almost every case. The only noteworthy exceptions to this are the ordinal and family curves for reptiles, is real, then their very sharp and unquestionably real Tertiary peaks are to be considered second peaks.

Omitting the dubious first (?) mammalian and second (?) reptilian peaks, the distribution by periods is as follows:

	Ordinal Peaks	Family Peaks	Generic Peaks
Tertiary	Mammalia (2?)	Osteichthyes 3 Mammalia (2?)	Osteichthyes 3 Mammalia (2?)
Cretaceous	Osteichthyes 3		Chondrichthyes 2
Jurassic	Chondrichthyes 2	Chondrichthyes 2	(Amphibia 2?)
Triassic	Osteichthyes 2 (Amphibia 2?)	Osteichthyes 2	Osteichthyes 2
Permian	Reptilia 1	Reptilia 1	Reptilia 1
Pennsylvanian		Amphibia 1	Amphibia 1
Mississippian	Amphibia 1	Chondrichthyes 1 Osteichthyes 1	Chondrichthyes 1 Osteichthyes 1
Devonian	Chondrichthyes 1 Osteichthyes 1	Placodermi	Placodermi
Silurian	Agnatha Placodermi	Agnatha	Agnatha

which maintain the peak level for two and three geologic periods, respectively. Some, but as yet insufficient, further analysis strongly suggests that this apparently exceptional feature in the reptilian record is an artifact caused by the coarseness of the time scale for the present graphs. If scaled to epochs or ages, it is highly probable that there was a drop in rate after the Permian peaks and that the apparent continuation of these peaks in the Triassic represents, in fact, a new rise in each curve. The reality of the Cretaceous drop in the mammalian curves is open to considerable question, yet this does agree with the usual trend of the other curves.

After the first peaks, the curves for the two earliest and most primitive classes decline more or less steadily to extinction (Placodermi) or near it (Agnatha, with a few living relicts but no fossil record after the Devonian). The Chondrichthyes have a clear-cut second peak on all three curves, and the Osteichthyes have not only a second but also a third peak. The Amphibia have slight but probably real second peaks for orders and for genera. There is no second peak in the present graphs for the Reptilia, but (as noted above) this is probably an artifact and second peaks probably did occur at each taxonomic level during the Mesozoic. If the Jurassic peak for mammals

The spaces are almost completely filled. In *every* period after that in which the phylum first appears (Ordovician), some class of vertebrates was in a phase of markedly rapid proliferation of new groups. Moreover this is true for each of the three taxonomic levels graphed except for orders in the Pennsylvanian and families in the Cretaceous. The apparent exceptions have little or no significance. A *class* of vertebrates (Reptilia) first appeared in the Pennsylvanian, and rates of appearance of new families were high in the Cretaceous (for Chondrichthyes, Osteichthyes, and Reptilia) even though still higher rates in adjacent periods keep these from appearing as peaks on the broadly generalized curves of the present graphs.

Thus, in the words of the original proposal for this symposium by L. G. Henbest, *within* a single class (and the same is true for smaller subdivisions not here graphed) there is definitely a tendency for "proliferations . . . to be segregated in particular epochs." As between different groups or for the Vertebrata as a whole, however, there is certainly no tendency for their times of most rapid diversification to coincide. The various segregated times of proliferation for each class or lesser group are so scattered through geologic time that one or more occurs in every period perti-

nent to this history. In this sense, "the proliferations are not segregated but are distributed more or less evenly through time."

This distribution of peaks of differentiation of new groups through time is more or less even, but it is not random. There are evident systematic relationships between the various peaks. Possible interpretations of this fact require further discussion, which follows on later pages.

SEQUENCE OF ORDINAL, FAMILY, AND GENERIC PEAKS

Within each class, there is a strong tendency for rates of appearance of new genera to rise and fall in the same sequence as the rates for orders, but to do so at later times. In the ten most clear-cut peaks seen in the graphs (figs. 2–3) a generic peak occurs one period later than the ordinal peak in six cases. The four apparent exceptions, which have ordinal and generic peaks in the same period, are probably not really such in any case but are artifacts of the presentation on a coarse time scale. In each case the generic peak was probably later than the ordinal peak by a considerable time and yet occurred in the same period. This is positively established for the Mammalia and is very clearly shown in the graph of epochs (fig. 3, bottom) rather than by periods. Ordinal and generic peaks occur in the same period, the Tertiary, but the former in the Paleocene and the latter in the Pliocene, with an interval of at least 45 million years between them.

The evidence is that a generic peak regularly (usually and perhaps always) occurs some 25 to 50 million years after an ordinal peak. In the case of the mammals, graphed with a more refined time scale, the family peak falls between those for orders and for genera, as might be expected. On the period scale, the family curve tends to parallel the generic rather closely and simultaneously. This perhaps reflects the classifier's frequent habit of treating a family simply as a bundle of genera, so that more genera automatically mean more families, whereas the number of orders recognized is largely independent of the number of genera. However that may be, further consideration of families can add little to conclusions from the relationships of appearance rates in orders or genera.

As vertebrate classification has been worked out and is reflected in these data, large categories such as orders represent basic and new adaptive types. Lines of descent from these normally diverge and involve adaptive radiation, but within the scope or building on the basis of the ancestral ordinal type. Families, genera, and other lower taxonomic units categorize the lesser adaptive types. They also include the many more or less adventitiously isolated groups, which reduplicate a type in a variety of localities and environments and which fill in many ecological niches within broadly similar life zones. The vertebrate record shows that the peak of splitting into basic types, as exemplified in rate of appearance of new orders, considerably precedes the similar peak of splitting into lesser groups, such as genera. When genera are appearing at their highest rate, the rate of appearance of orders is dropping rapidly. As regards total numbers of taxonomic units, also, in a given group (as a rule) when the number of orders is highest, the number of genera is lower than it later becomes. Past the ordinal peak, the number of orders tends to decrease as the number of genera increases.

Now, in studying the supposed phenomenon of "explosive" evolution and testing possible correlation of this with physical events, when does the "explosion" occur? By definition, the "explosion" is a relatively abrupt increase in numbers of taxonomic units, or in their rate of appearance. In absolute numbers, genera and species are most numerous and they are also at the level of usual taxonomic study. The "explosion" is commonly taken to be an increase at this level. But peaks of incidence of new genera follow those of new orders with such regularity in the record here presented that it seems inescapable that the fundamental event, in some sense the cause of the expansion, is the earlier ordinal differentiation. Then seeming correlation of generic "explosion" with contemporaneous physical events would appear to be purely adventitious, because the generic expansion was the outcome of events of some 25 or 50 million years earlier.

In fact, it becomes impossible to pin down the essential point of this chain to any particular expansive phase in it. A most fundamental adaptive type categorized as

a class appears and in 25 to 50 million years its rate of ordinal differentiation reaches an "explosive climax." In another 25 or 50 million years the rate of generic differentiation reaches a similar but quite distinct climax. The whole process seems to be a biological, evolutionary sequence affecting all vertebrates throughout the history of the group. It naturally occurs against the background and within the limitations of the physical environment, but it seems impossible even to make a start at realistic correlation of so regular and continuous a process with intermittent tectonic episodes. The occurrences of second and third climaxes within a given class fall into exactly the same sort of sequence, for without exception they also are initiated by emergence of new adaptive or structural types which simply do not happen, in our classifications, to be formalized at the rank of classes. Once they arise, a sequence of ordinal and generic highs follows in due course as it did after the class as a whole arose.

The second peaks of the Chondrichthyes involve the appearance of "higher" or "modernized" sharks and rays: galeoids, squaloids, and batoids. Those of the Osteichthyes followed the appearance of the subholostean-holostean structural lines. The third peaks of the Osteichthyes follow the appearance of teleosts, now the dominant fishes.

In the probable but not absolutely established occurrence of two peaks of reptilian differentiation, one late Paleozoic and one early Mesozoic, the first involves the cotylosaurian-synapsid level (the two groups being adaptively and structurally very similar although their different fates have caused their radical separation in the usual classifications). The second set of peaks follows in regular sequence after appearance of the archosaurian level of organization in the Triassic.

A classic example of supposed "explosive" evolution and its correlation with diastrophism is the "explosion" of mammals supposed to initiate the Cenozoic and to be simultaneous with if not caused by the Laramide Revolution. But in fact the most basic event, the origin of placentals, occurred sometime well before the end of the Cretaceous. Most of the orders of early Cenozoic mammals did not appear at the Cretaceous-Paleocene boundary, but straggled in over a span of some 20 million years. The rate of appearance of new genera was low in the Paleocene and it did not reach its climax, its most truly "explosive" phase, until the Pliocene, perhaps 60 million years after the end of the Cretaceous. When did the "explosion" occur? Certainly not at the Cretaceous-Paleocene boundary, and claimed relationship to the Laramide Revolution must surely be viewed with suspicion.

The most fundamental events of all within the span of vertebrate history, the origins of the classes, are not "explosions" in any sense, since each class is rare and little varied when it first appears, but these most major first appearances also follow a biologic sequence which seems to have no possible correlation with tectonic episodes dividing the periods and eras. Such appearances do not regularly occur at the beginning of periods. The Agnatha appear in the middle (or possibly late) Ordovician, Placodermi in late Silurian, Chondrichthyes and Osteichthyes in early Devonian, Amphibia in late Devonian, Reptilia in middle or late Pennsylvanian, Aves and Mammalia in middle Jurassic. (Mammals may have appeared in the late Triassic, as usually stated, but at present most of the supposed Triassic mammals appear to be reptiles by definition, and all may be.) Although some, at least, of these classes may have originated considerably before their first known appearances, it would be purely arbitrary to postulate origins at times of preceding diastrophic climaxes. Moreover no class of vertebrates and few of the major structural grades within the classes appear during or immediately after the two greatest tectonic episodes of the span of vertebrate history, the Appalachian Revolution and the Laramide Revolution.

SUCCESSION AND REPLACEMENT

The climaxes or peaks of rate of appearance of new groups among the vertebrate classes form a fairly regular progression which clearly is not random. Or rather, they form two progressions, one for the primarily finned, aquatic types, the "fishes" (Classes Agnatha, Placodermi, Chondrichthyes, and Osteichthyes), and one for the primarily footed, amphibious to terrestrial types, the

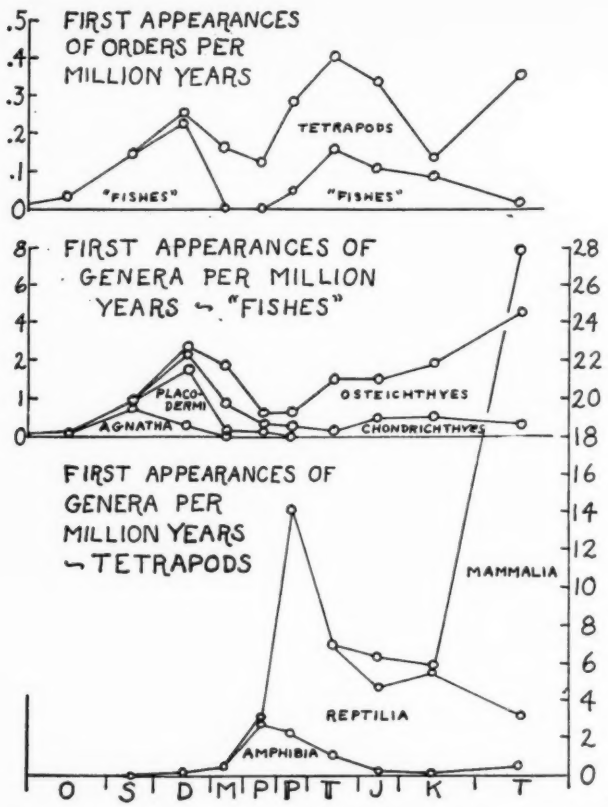

FIG. 4—Graphs of first appearances of orders per million years for vertebrates as a whole and of first appearances of genera per million years for "fishes" and for tetrapods. Time scale and general convention of construction as in Figs. 2–3.

tetrapods (classes Amphibia, Reptilia, and Mammalia, with the Aves, not here discussed, forming a separate major ecological type of their own).

The succession involved here seems, again, to be evolutionary in a sense primarily biological and I see no clear evidence for correlation of its main events with purely physical changes such as mountain-building. The most probable interpretation seems to be that at intervals some branch from an earlier radiation reaches a superior adaptive status which enables it largely (seldom completely) to replace earlier forms living over somewhat the same environmental range. In taxonomic terms, a new class, subclass, or superorder arises and the sequence of ordinal down to generic and specific "explosive" phases follows, as outlined above.

The sequence of such phases in the Agnatha, Placodermi, and Chondrichthyes plus Osteichthyes is quite clear from Ordovician to about the end of the Paleozoic. (See figs. 2, 4.) The ordinal climax of each group coincides approximately with the generic climax of the preceding group. In the Pennsylvanian and Permian, with no radically different or successional new adaptive type on the scene, the rates of appearances of new groups in Chondrichthyes and Osteichthyes fall to low points and evolution of "fishes" becomes relatively stagnant. In this part of their history, Devonian through Permian, Chondrichthyes and Osteichthyes are not successional to each other but simultaneous and closely parallel in the rise and fall of rates of appearances. The two, together, and not either separately or each in succession, seem to replace the earlier "fishes." There is, in fact, evidence that most Chondrichthyes were then marine and most Osteichthyes freshwater, so that they parceled out the aquatic domain between them.

In the Mesozoic and Cenozoic, as many Osteichthyes became marine, there is no longer simultaneity in "explosions" of these two classes, but a complex succession seesawing from Osteichthyes in the Triassic to Chondrichthyes in the Jurassic to Cretaceous and back to Osteichthyes in the Cretaceous to Recent.

Succession of "explosive" episodes among the tetrapods is simpler and rather obvious throughout. (See figs. 3–4.) The only complications in the Amphibian-Reptile-Mammal sequence are in relatively minor points and need not be discussed in this broader summary.

EXTINCTIONS, SURVIVALS, AND TOTALS

Although this study is mainly devoted to episodes of appearance of new groups of vertebrates, some of the more striking, related features of total expansion and contraction may be briefly mentioned.

Changes in total numbers of taxonomic units between any two times depend on a balance of four factors:

(1) Splitting up of single groups into two or more.
(2) Transformation of single groups to the point recognized as origin of new groups at the same taxonomic level.
(3) Survival of groups without change sufficient for recognition at the given taxonomic level.
(4) Disappearance of groups, without known descendants.

As the data are usually set up, these factors are not clearly distinguishable and cannot be accurately analyzed. Such analysis can be made (although even here with some difficulty in categorization) for a few, small, exceptionally well known and well studied groups, such as the horses. For most groups and particularly for large groups such as those involved in the present summary, the data do not as yet exist, or are so incomplete that they would not repay the great labor of accurate analysis. In broader studies at present, therefore, the data used reflect the interplay of these factors but do not adequately indicate the contribution of each. "First appearances" include contributions from both (1) and (2), without distinction, although (1) increases the total and (2) does not. In a continuous sequence, the number of first appearances due to (2) increases with the length of the time unit used, although this misleading effect can be eliminated if first appearances are plotted relative to time, as in most of the graphs here presented.

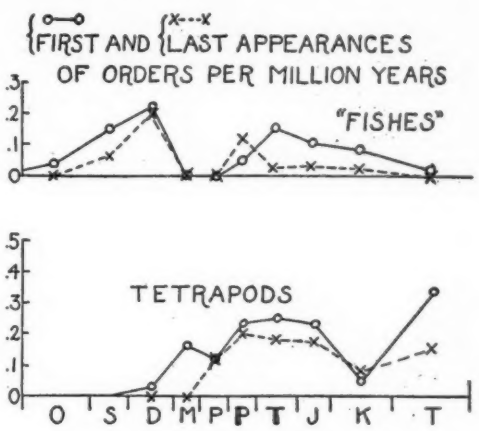

FIG. 5—Graphs of first and last appearances of orders per million years in "fishes" and in tetrapods. Time scale and general construction as in Figs. *2–4*.

"Last appearances" include contributions from both (2) and (4), again without distinction, although those due to (4) decrease the (subsequent) total and those due to (2) do not. Again, the last appearances due to transformation, (2), tend to be proportional to the time covered and their real significance is not evident unless they are plotted relative to time. First and last appearances due to (2) are equal in number and balance each other exactly. The last appearances in any given time unit affect the total not in the same but in the following time unit.

Survivals from one time unit to the next, (3), tend to maintain the total level without change and are readily tabulated but are of obscure and variable significance. The number of survivals obviously decreases greatly as the length of the (essentially arbitrary) used time unit increases, and this confusing effect cannot be eliminated simply by plotting survivals relative to time. (In fact, this merely exaggerates the defect; plotting the reciprocal figure does give a more reliable result, but one still difficult to comprehend and interpret.) The tabulation or plotting of survivals has little or no clear significance unless the time unit used is considerably shorter than the average time span of the taxonomic unit used. Since the average span of vertebrate genera is less than that of a geological period, study of survival in genera is not useful on the scale of broad summary used in the present short contribution. Orders of vertebrates do tend to persist con-

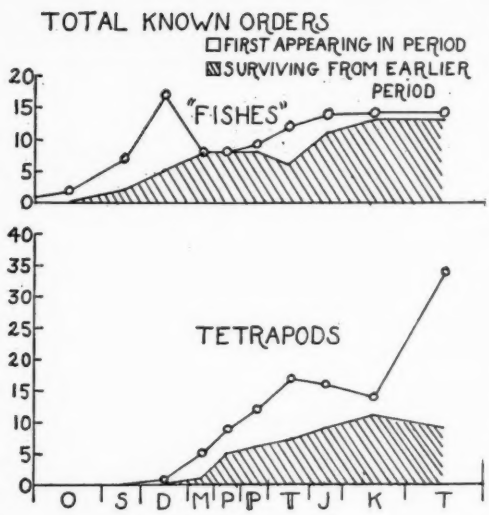

FIG. 6.—Graphs of numbers of known orders of "fishes" and of tetrapods. The absolute total, not the number per million years, is indicated for each period. The height of the line above the cross-hatched area indicates the part contributed to the total by orders surviving from earlier periods. Time scale as in Figs. 2–5.

siderably longer than one geological period and so study of their survival from one period to another does have some usefulness (see fig. 6 and text, below).

Figures for last appearances of genera or other small taxonomic units tend, unless the time scale used is more refined than is generally practicable for large groups, simply to run parallel to the figures for first appearances. This has two causes. First, the last appearances due to (2) in the list of factors given above are always equal in number to first appearances from the same cause and occur, theoretically, at the same point in time. Second, last appearances representing true extinction, (4), tend to be proportional to total numbers and to be accelerated by increase in first appearances. There is normally a time lag in this case, but in the case of smaller taxonomic units it may be too short to be clear unless the data are quite exceptionally good and a brief time unit can be used.

Even at the level of orders, figures for first and for last appearances tend to run parallel (fig. 5), although some significant interplay can be seen. For "fishes" the Devonian was a time of maximum rates both for first and for last appearances. This is a reflection of replacement. The peak of first appearances is due to rise of the Chondrichthyes and Osteichthyes and the peak of last appearances is due to waning of the Agnatha and Placodermi. In the Mississippian and Pennsylvanian both first and last appearances of orders of "fishes" dropped to a minimum. (For genera, this minimum was Pennsylvanian to Permian, see fig. 2.) During this time, the successful forms in the Devonian competition simply tended to survive with relatively little change. In the Permian, last appearances increased markedly without equal increase in first appearances; this is the only period in which last appearances were more numerous than first appearances of orders of "fishes." In combination with the drop of last appearances and rise of first appearances in the Triassic, this reflects a radical turnover of basic types of "fishes" from Permian to Triassic. After the Triassic there are no marked changes. Both first and last appearances of orders dropped steadily (and first appearances and totals of genera rose steadily) as the broad structural grades introduced in the Triassic survived and proliferated at lower taxonomic levels.

Among tetrapods, the equal first and last appearance rates of the Pennsylvanian and high for both in the Permian and Triassic accompany rapid turnover among early amphibians and reptiles and the beginning of replacement of some of the former by the latter. The drop in both rates in the Cretaceous, with last appearances becoming for the only time more frequent than first appearances, followed by a rise of first appearances far above last, repeats in geologically briefer time and with some differences the sort of episode seen among fishes in the late Paleozoic and early Mesozoic.

The total of known groups at any time is of course the sum of first appearances and survivors from the preceding time unit (fig. 6). The number of survivors, in turn, is the total for the last period minus last appearances in that period. As regards orders, the course and balance of these various factors and their results are sufficiently shown in figs. 5–6.

In view of the picture as a whole, several periods of major evolutionary activity of different sorts stand out. The most striking of these seem to be:

DEVONIAN: Rapid turnover from earlier to later major groups of "fishes." High extinction rates for older types.

Extremely high basic origination rates for many sorts of "fishes," to be followed in subsequent periods by their diversification in lower taxonomic categories.

Origin of tetrapods.

PERMIAN TO TRIASSIC: Among both "fishes" and tetrapods, strongly pronounced turnover, with high last appearance rates in the Permian, at least, and high first appearance rates in the Triassic. (These major changes concern mainly the Osteichthyes and the Reptilia.)

CRETACEOUS TO TERTIARY: No definite climax or crisis among "fishes," but strongly marked tetrapod turnover involved in decline of the reptiles and rise of the mammals.

It has long been realized that these were major episodes in vertebrate history and the present conclusion only confirms and to some extent quantifies what was already well-known. It should, however, be emphasized that these episodes are of long continuation and that they are not sharply defined in time, even as to their beginnings. It has, for instance, already been stressed that the essential features of the Cretaceous-Tertiary crisis cannot really be localized just at the boundary between those periods. The episodes are parts of a long and essentially continuous process.

The Permian-Triassic and Cretaceous-Tertiary major evolutionary changes do coincide with era boundaries, or, rather, the accepted era boundaries occur within the long and vaguely defined span embracing these evolutionary events. The era boundaries, in turn, coincide with mooted major tectonic episodes, the reality or true nature and extent of which are for others to judge. There may be some degree of causal connection within the complex totality of evolutionary processes involved and it is unlikely that physical events played no part in these evolutionary episodes. The conclusion that theirs was the decisive and necessary part is not supported by the biological evidence and may be gratuitous. It is also to be remembered that the era boundaries were established in large part on paleontological grounds, so that their coincidence with evolutionary events is not really, in another sense of the word, a coincidence.

CONCLUSIONS

In certain particular cases, strong or even startling evolutionary effects can be clearly traced to physical, geographic and tectonic causes. Completion of the Central American land bridge in the Pliocene was followed by geologically sudden and radical changes in the fauna of South America. Rates of extinction rose rapidly among native South American groups of mammals, particularly, and rates of diversification or proliferation became extremely rapid among groups introduced from North America. Similar results followed rise of the Bering bridge between the Old World and the New in the late Eocene after long isolation through the middle parts of the period. In such cases the correlation of biological and physical events is obviously real. It is clear that such events have repeatedly occurred and constitute a large and important part of the history of life. They do not, however, as far as can be seen, account for the origins of important new types or structural grades of animals. The episodes of proliferation that follow them are also of secondary importance in the whole picture of earth history. Even when continent-wide, they are local with respect to the earth as a whole, and the proliferation is on low taxonomic levels, dispersion into new living spaces generally by replacement of older, ecologically similar, and often more or less closely related previous residents.

The physical concomitants of such episodes are also and still more strictly local. Relatively slight local warping of the crust in a small area of Central America or of the Bering region, for instance, is all that need occur. No widespread or major diastrophic crisis is required or is evidenced. On the other hand, world-wide and revolutionary orogeny and diastrophism could occur without having any particular results of this sort, because it need not affect the small areas that happen to be crucial. It is significant that the two examples given above (and many others that could be added) did not occur at times of disturbances or revolutions usually recognized by adherents of the theory of periodic world-wide diastrophism and did not occur at or shortly after conventional epoch or period boundaries.

It is probable that such events are sometimes involved in episodes that are important details in the broader picture of biological history. This may be true, for instance,

of the changes used in fixing the Cretaceous-Tertiary boundary, especially disappearance of the last dinosaurs and appearance of a meager vanguard of Cenozoic mammalian types in the (few and local) collecting regions where these facts can be ascertained. The geographic event may then have determined a useful time datum and may enable us to draw a boundary in a given region. Still that is not evidence that the geographic event itself was more than a local crustal warp someplace or other, or that it did more than set the precise time of evolutionary events that would in any case have occurred at about that time in the sweep of the long, continuous evolutionary process.

The evidence summarized in this paper is consistent with the view that most of the broad features of vertebrate history might have been much the same if the earth's crust had been static (providing that the surface remained sufficiently varied and with large connected and nearly connected land and sea areas). Crustal movements may have had essential roles only as regards details of timing and of distribution, important details in some cases but still only details. The older and still perhaps more common belief in causal synchronism of periodic world-wide evolutionary and diastrophic episodes is certainly not disproven, but the evidence runs rather more against than for it. The most likely points at which physical events may have had decisive influence are the extinctions of aquatic vertebrates around the end of the Permian and of terrestrial vertebrates around the end of the Cretaceous.

There is a well-marked periodicity in vertebrate history, especially as regards successive peaks and valleys of high and low proliferation of new groups, in one class after another or sometimes within one class at different times. Taken as a whole, these peaks are rather evenly distributed in geologic time and have no clear segregation that could correspond with periodic crustal crises. Within any one major group, the peaks at different levels of adaptive differentiation spread very widely in geologic time, over spans up to 100 million years or more, which makes difficult or impossible their connection with particular tectonic events more sharply defined, as at period boundaries. The regularity of this long process is, moreover, suggestive of continuity of evolutionary forces acting regardless of periodic physical events despite the periodicity of some of the results. The "explosions" in evolution are not really isolated occurrences or brief even in the sense of a few million years of geologic time. They seem, rather, to be merely regular, shorter episodes or manifestations in a more basic process which is really secular and not periodic.

The origins of classes, orders, or other taxonomic units, either singly or in the accelerated clusters of "explosions," do not, in the record, show any apparently causal correlation with epoch or period boundaries, beyond the extent to which these boundaries have themselves been set to correspond with some convenient evolutionary marker. The important Paleozoic-Mesozoic boundary, for instance, occurs within and near the climax of a radical faunal change, which is used to define that boundary, but it does not coincide with, or even approximate, the time of origin of any basic new type of vertebrate or any peak in proliferation of some group. It is marked mainly by negative, not positive, evolution, by extinction. The subsequent positive faunal changes may have been stimulated by preceding extinctions but may also have been the outcome of events that occurred much earlier or indeed of a whole chain of events back to the origin of the vertebrates or of life.

As far as this evidence goes, then, diastrophism and other physical events continue to hold a place in the totality of factors that are, inseparably, the cause of evolution. They cannot be promoted to a role as leading and distinct cause of the major features of vertebrate evolution. The related but different and more particular theory of accelerated evolution during rhythmic or periodic diastrophic disturbances or revolutions deserves, at best, a verdict of "not proven." For the vertebrates, at least, it may be proper to add "improbable."

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PERIODICITY IN INVERTEBRATE EVOLUTION

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ABSTRACT—Varying rates of evolution in the main groups of fossil invertebrates are estimated by means of graphs showing distributions of genera through geologic time. There are from one to three peaks in each group which appear to represent times of relatively rapid differentiation. These are followed by depressions when evolutionary activity was reduced. Several groups show similarity of pattern which suggests common causes. In the majority of groups there was a particularly marked depression in evolutionary rates in the late Paleozoic. Nearly all of the geologic periods were marked by peaks of evolutionary activity in one or more major groups, but the Ordovician, Mississippian and Jurassic periods were times of peak activity in many groups. Causes for these fluctuations undoubtedly are complex and include both biological and physical factors. Of the latter, probably the most important were the successive expansions and restrictions of shallow epicontinental seas. These always have been the chief centers of evolution of marine invertebrates and they were greatly reduced or eliminated by simultaneous emergence of the continents. It is believed that the evolutionary peaks coincide with times of rapid expansion into evolutionary niches previously vacated by extensive extinctions. Diastrophism influences the course of evolution by causing extinction, migrations and modifications in habitats, but there is no evidence that there is increased evolutionary activity during diastrophic disturbances; in fact, the converse may well be true.

INTRODUCTION AND ACKNOWLEDGMENTS

ACCORDING to a view endorsed by some students of earth history, organisms tend to undergo accelerated evolution when subjected to widespread environmental changes such as those thought to result from orogenic cycles. This theory is supposed to explain marked floral and faunal changes at major stratigraphic boundaries. Diastrophic revolutions by causing changes in environments are supposed to stimulate evolution, presumably by increasing the differential stresses of natural selection. On the other hand, experienced stratigraphers have been heard to say that one paleontologic break is about as important as another; that our classification of geologic time is largely arbitrary.

The present inquiry is devoted to a test of these debatable points of view. It is proposed to examine the paleontological records of the better known groups of fossil invertebrates, in order to determine whether or not there have been times characterized by prevalently high or low evolutionary rates among marine invertebrates. Furthermore, the record will be examined for close correspondence between evolutionary peaks and times of general diastrophic climax.

Limited to the objectives of this symposium, the present study is extracted from a larger investigation of animal evolution in collaboration with George Gaylord Simpson. Some of the data on better known groups of fossil invertebrates are analyzed in search of indications of evolutionary periodicity.

Several specialists generously have contributed lists of raw data used in preparation of the graphs presented here. They are: Foraminifera—W. S. Cole, H. E. Thalmann, M. L. Thompson; Anthozoa—J. W. Wells, R. C. Moore, M. LeCompte, E. C. Stumm; Bryozoa—R. C. Moore, M. Fritz, A. Loeblich, A. McNair; Crinoidea—R. C. Moore; Cephalopoda—A. K. Miller, R. H. Flower, C. Teichert, A. G. Fischer, O. H. Haas; Gastropoda—K. V. W. Palmer, J. B. Knight; Ostracoda—B. K. Nadeau, P. G. S. Bradley, H. N. Coryell; Trilobita—B. F. Howell, H. B. Whittington, R. and E. Richter, J. M. Weller.

NATURE OF THE DATA

The fossil record, from which inferences about evolution may be drawn, is neither complete, nor uniformly good. New discoveries and revised interpretations have

resulted in more or less continuous changes in our conclusions. However, in spite of the fact that paleontological knowledge is now and will continue to be in a state of flux for a long time, conclusions for the better known groups are reasonably stable. Imperfect as it is, the record of fossil invertebrates is an impressive one, and probably is an adequate sample of the evolutionary history of the better known groups.

There are numerous, obvious sources of error to be assessed in this type of study, and many of these have been considered and allowed for in the tabulations. The data are heterogeneous in quality. For instance the majority of groups have not been recently revised, so that there is uncertainty regarding the proportions of unrecognized synonyms and homonyms to valid genera. Probably many of the names used in the compilations belong to unrecognizable genera, hence, are meaningless. Some groups are more thoroughly studied than others, therefore, they contain relatively more genera. It is believed that such sources of error may account for deviations from the actual proportions of biologic genera in various groups. It is futile to guess at the total numbers of genera that ultimately will be known in each group, but it seems that they may exceed present estimates by several hundred per cent in the best known orders.

Some geologic systems probably are not as thoroughly sampled as are others. In some instances this may be due to lack of development of suitable facies in readily accessible areas. Unevenness in sampling, of course, is being smoothed out with time.

Our record of invertebrate evolution is mainly that of marine groups. Fossiliferous marine strata correspond with times of invasion of continental areas by seas which generally were shallow and otherwise unlike the environments of the oceans. The most extensive inundations left the most widespread fossil record, and consequently faunas from these maximum floods tend to be better known than the faunas from other epochs. It should follow, logically, that if the times of most extensive submergence correspond with the better known marine faunas, then they also would correspond with times of peak diversity, because faunas tend to become apparently more diverse as they are studied. This is not necessarily the case, however, because the Cretaceous period, outstanding as a time of unusually extensive submergence of the present continental areas, was not a period of very high rates of generic differentiation.

Probably the greatest potential source of error lies in the stratigraphic bias with which invertebrate paleontologists nearly always work. Most of the great monographs are limited to the fossil forms of stratigraphic units, with little or no regard to the ancestors and descendants of these animals. As an example, a large proportion of the known Jurassic genera of brachiopods were proposed in a few published works. Our graphs reveal an apparent burst of evolutionary activity among Jurassic brachiopods, and this may or may not be artificial. The independent conclusions of many specialists working over the whole field of Mesozoic brachiopods is required. Unfortunately, the number of students of systematic invertebrate paleontology has been so small in comparison with the task that a half century may elapse before the work of one investigator is critically reviewed by another. The prevalent preoccupation with "guide fossils" has always impeded growth of knowledge concerning the evolution of invertebrates, and, anomalously, this limits stratigraphic value of fossils.

Naturally, strict evaluation of these and other sources of error are at present impossible. Nevertheless, the regularity of certain trends and patterns exhibited by the data appear to be independent of any of the more obvious sources of error. I believe that we can draw from these data useful clues regarding the facts of invertebrate evolution.

Two additional possible sources of systematic error have been considered. A large error in estimates of the *relative* length of a geologic period would, of course, produce an apparent simultaneous fluctuation in all groups of organisms. While this is admittedly a probable source of error, the magnitude of such errors appears to be too small to account for some of the more striking fluctuations in the records. For example, the Pennsylvanian period appears to have been a time of relatively low rates of generic differentiation in most invertebrate groups. Theoretically, the evolutionary slump indi-

cated in the graphs might be an artifact resulting from an excessive estimate of 200–300% of the length of Pennsylvanian time. Although it cannot at present be demonstrated that such an error of estimate does not exist, it appears that the relative magnitude of the rocks of the Pennsylvanian and Mississippian systems over the world are not greatly disparate. There is no independent evidence that the two periods differed greatly in duration, even though several times as many genera first appeared in the Mississippian as compared with the Pennsylvanian period.

A second possible source of error, suggested to me by Dr. J. Brookes Knight is the basic assumption followed here, that the known prevalent faunal characteristics of each system, as considered on a global scale, fairly represent the marine faunas of the time, rather than particular limited facies. It is here assumed that the benthonic invertebrate faunas in the past, as at present, were richest in numbers and variety in the epicontinental seas (epeiric and shelf seas), and that the stratigraphic record as we know it, mainly is the record of those seas.

These are assumptions, true, but there is no reason, it appears to me, to doubt that the marine faunas known for instance, from the Pennsylvanian and lower Triassic rocks in many scattered parts of the world, are not adequately representative of the shallow water faunas of those periods. The special characteristics of these faunas, in my opinion, result from world conditions, not from conditions of local environment (facies).

In the following graphs numbers of known genera are given by periods, rather than epochs. This conceals fluctuations within periods, but at the same time tends to smooth irregularities related to facies. For the present purpose the Pleistocene is included with the Tertiary.

ERUPTIVE EVOLUTION

Evolutionary outbursts, or eruptions, have been defined as the "relatively sudden breaking out of evolutionary diversification within any group of organisms" (Cloud, 1948). This requires elaboration. In the first place, it is necessary to define the manner in which evolutionary diversification is to be measured. Secondly, it is not clear exactly what is to be understood by the expression "relatively sudden."

An evolutionary eruption involving an entire phylum or class involves much more time than an outburst at the level of an order or a family. It seems that the rate of outburst probably varies inversely with the rank of the group under study.

Several methods theoretically are available for assessing evolutionary rates in fossil organisms, but by far the most practical is a simple measurement of rate of differentiation of genera. The genus, not the species, is still the working unit of the paleontologist. At the present, the genus is taxonomically more stable than the species, and because of its wide geographic range, as compared with that of the species, the genus receives international attention, whereas the species does not. As a result it is virtually impossible to obtain extensive regional data on more than a very few fossil species. They seem remarkably provincial as compared with living forms. Descriptions of fossil invertebrate species are not now adequate for general discrimination of synonyms and subspecies.

Disadvantages in use of the genus as an evolutionary unit are evident. Mutation and selection directly affect populations, but not genera. Populations, in turn, form species and, collectively, species make up genera. The genus is well above the level at which evolutionary processes effectively operate. Nevertheless, the genus *is* a product of evolution and, therefore, fluctuations at the generic level probably accurately reflect evolutionary fluctuations at lower levels.

THE GRAPHS

In the present study the distributions of fossil genera in time are shown in two sets of graphs. In the first are shown the average total numbers of genera, and rates at which new genera appear. In the second series of graphs is shown the fluctuating percentage of new genera to total numbers through time.

The total number of related genera existing at one time equals the number of survivors from the preceding geologic age plus newly evolved genera. Thus, it is the changing difference between additions and ex-

tinctions which is responsible for fluctuations in total numbers of genera. Now, other things being equal, the total numbers of genera tend to vary with the rates at which new genera appear (fig. 1). Figure 1 and following graphs show that fluctuations in the total number of Foraminifera, ostracodes, graptolites and others, roughly parallel curves of the rate of appearance of new genera. If the rate of new appearances of genera falls below the rate of extinctions, the total number will decrease, and vice versa. The totals will be greatest when new genera appear most rapidly and conversely, assuming constant rates of extinction.

Fluctuations in total numbers are caused by varying rates of both evolution and extinction, and these two processes bear no simple relationship to each other. Rise in rates of differentiation and in total numbers do not always indicate acceleration in the evolutionary processes. If we postulate constant rates of evolution, for sake of illustration, then all of the fluctuations in numbers and apparent rates of differentiation might merely reflect fluctuating extinction rates. Of course, this is not plausible as will be shown presently.

Supplementary data are needed for distinguishing between fluctuations of evolutionary rates and those of extinction rates. In this connection, graphs representing fluctuations in the ratio of new to total genera are helpful because a real acceleration in evolution necessarily involves a rise in relative numbers of new genera in a fauna. As long-ranging genera accumulate, however, the new to total ratio of genera gradually drops so that the high point on the new/total graph will commonly mark the earliest part rather than the peak of an evolutionary burst.

From the foregoing it appears that essential characteristics of an evolutionary eruption in any group are: 1) Marked increase in total diversity, 2) increase in mean rate of diversification, and 3) a rise in percentage of new to surviving genera early in the eruption.

Records of several of the more important groups of fossil invertebrates are presented below.

RECORDS OF MAJOR GROUPS

Foraminifera.—A slump in the foraminiferal record is shown in the Devonian (fig. 1). This may be an artifact related to insufficient attention to Devonian rocks. However, several other groups show a decline at the same time. A second decline following a Permian peak and reaching a low point in the Triassic is real, as also is the spectacular climb to high rates in the Tertiary, when the Foraminifera reach a mean rate of differentiation of nearly seven genera per million years. This is a high mean rate of evolution for any order of invertebrates, but it is only one-fourth the rate attained by Simpson's mammals during the same period.

Most of the suborders of Foraminifera appeared in the Pennsylvanian, one period before the first major peak in the Permian. By the close of the Paleozoic all major groups (suborders of Glaessner, 1947) had appeared.

Ostracoda.—The ostracodes (fig. 1) show three low peaks in the Ordovician, Mississippian, and Jurassic. A slump in the Triassic is well defined, and reflects the general rarity of ostracodes in rocks of this period. The peaks appear to correspond well with the introduction of new families in or just before the Ordovician, Mississippian, and Jurassic.

Graptolithina.—The true graptolites, or Graptoloidea (fig. 1) reached the peak rate of differentiation in the Ordovician, the period of origin, and they became extinct in the following period. The dendroid graptolites had a longer history, with a well defined peak of activity in the Silurian, finally becoming extinct in the Pennsylvanian. Note that the vertical scale is given in tenths rather than unit genera. Mean rate of differentiation of graptolite genera was slow at the scales used in plotting the graphs.

Bryozoa.—The record of the Bryozoa (fig. 2) is unlike those of the preceding groups. One of the classes appeared relatively late in the history of the phylum. A single class appears to be represented in the Cambrian, and three additional classes appear in the Ordovician. The fifth class does not certainly appear until the Cretaceous, even though certain Paleozoic forms are referred to it. Ordovician, Mississippian, and Cretaceous peaks possibly correspond with the appearances of new adaptive types, but low rates over long spans of time charac-

terize the evolution of the phylum as a whole. The first and third peaks certainly are related to appearances in the same periods of three out of the five classes. The Pennsylvanian-to-Triassic depression apparently is real.

The history of the Cyclostomata is remarkable. Appearing in the Cambrian, this class produced genera at a very low mean rate of less than one genus in 4,000,000 years through the Paleozoic and earliest Mesozoic. Rising sharply through the Jurassic the class reached a peak of activity in the Cretaceous, when a mean rate of about 9 genera per 4,000,000 years was attained. Perhaps this group was inhibited by competition until an environmental niche was opened up by disappearance of competitors. Such competing forms may have been the cryptostomes and trepostomes, which became extinct at the close of the Paleozoic. If so, the rise of the cyclostomes was long delayed.

Anthozoa.—Corals (fig. 3) show four well-defined peaks in absolute rates of generic differentiation in the Silurian, Mississippian, Permian and Jurassic. These are separated by well-defined depressions, of which those of the Pennsylvanian and Triassic are most pronounced (see figs. 3 and 10). No corals at all are known in the lower Triassic, and they did not become numerous or diverse until later in the period. The first and last of the peaks follow directly after the introduction of new orders and coincide with the appearance of many new families. The Mississippian peak involves the introduction of several families. The Permian peak, as will be shown later (fig. 10) did not involve increase in the relative numbers of

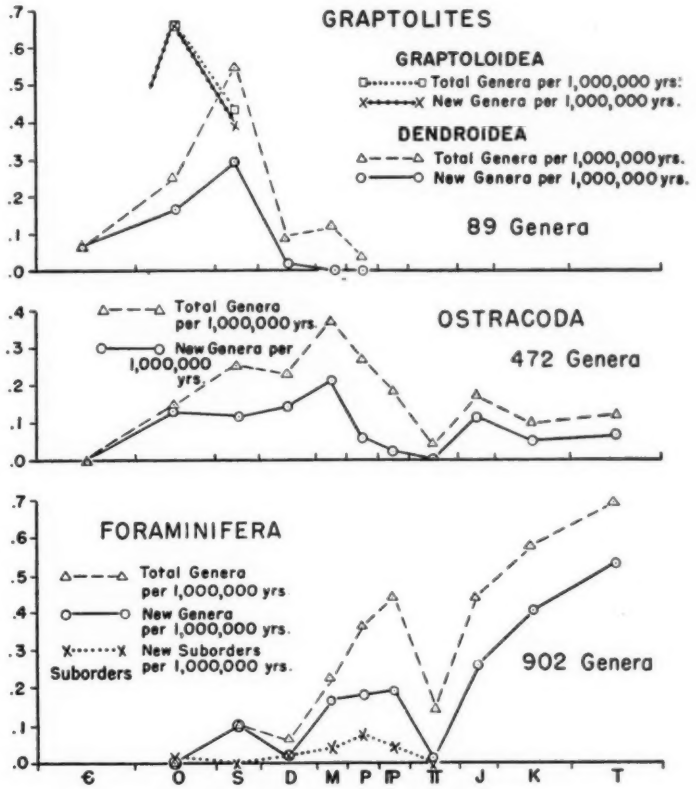

FIG. 1—Graptolites, ostracodes, and Foraminifera. Graphs showing total numbers of genera and numbers of new genera per million years through geologic time.

new genera. Therefore, it does not clearly mark an evolutionary burst.

Brachiopoda.—Brachiopod evolution (fig. 4) is characterized by steady ascent from the Cambrian to sustained moderate rates of generic differentiation, forming a plateau during the periods from the Ordovician to the Mississippian, inclusive, and a high peak in the Jurassic. The Pennsylvanian, Permian and Triassic periods lie in a flat depression as also do the Cretaceous and

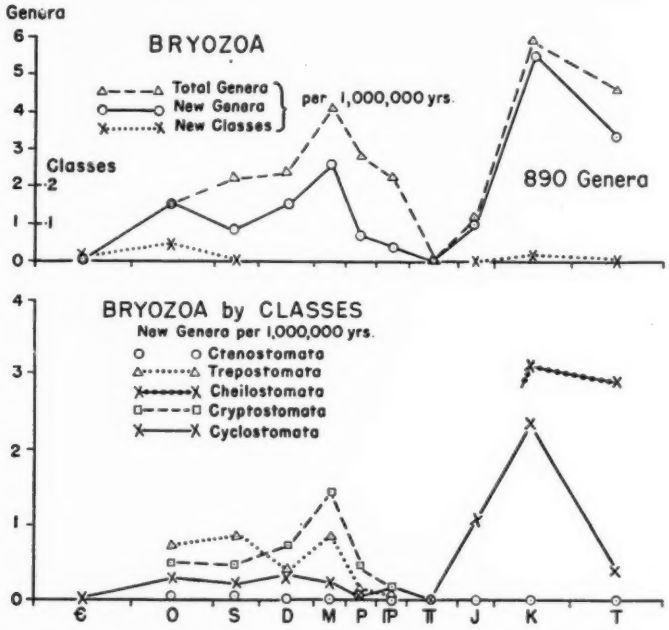

FIG. 2—Bryozoa. Total number of genera and numbers of new genera per million years.

Tertiary. By the close of the Devonian all of the brachiopod superfamilies were established. However, the peak rate of superfamily differentiation was in the Ordovician, followed afterward mainly by generic expansion. The graphs of the two great classes of brachiopods suggest something of competition during the early Paleozoic. That is, the inarticulates show marked decline while the articulates were on the increase. Brachiopod students are not certain about the significance of the Jurassic expansion. Possibly it is an artifact resulting from excessive generic splitting.

Crinoidea.—Crinoids (fig. 4) show four distinct peaks of which the first and fourth closely follow the introduction of new orders and probably represent the usual expansion at a new adaptive level. The second appears to be related to expansion at the family level. The third peak is related to a decreasing extinction rate. So, it is not interpreted here as a significant burst. There is no increase in percentage of new genera in the fauna. In any case the record appears to fluctuate markedly from lows to highs.

Blastoidea and *Cystoidea.*—The blastoids and cystoids (fig. 5) have somewhat contrasting patterns, and it may be that competition for similar ecologic requirements caused the demise of the cystoids before the decline of the blastoids. Both groups are characterized by low rates of differentiation, and their patterns are not closely like that of the crinoids. Fluctuations of the new/total ratio of genera in the three groups, however, as shown later (fig. 10) are similar.

Echinoidea.—The echinoid pattern (fig. 5) is distinctive. The Paleozoic part of the record shows sustained low rates of differentiation, and is similar to that of the blastoids. From Ordovician to Triassic times differentiation was slow and total numbers

of genera were small. With the development of more efficient adaptive types in the Triassic and Jurassic, comprising several new orders, the echinoids show impressive evolutionary activity as compared with their very conservative Paleozoic record. Noteworthy is the indication that the Permian-Triassic interval, so critical for many groups, did not deplete the echinoids. The "irregular" group, a new adaptive type appearing first in the upper Triassic rocks, does not reach peak diversity until the Cretaceous two periods later.

Cephalopoda.—The three main subclasses or orders of fossil cephalopods (fig. 6) show interesting trends. The Nautiloidea, originating in the late Cambrian, rose to an all-time peak in the Ordovician, descending from that time with minor variations, to the Recent. The Ammonoidea, on the other hand, got off to a good start in the Devonian, but did not reach a substantial climax until the Jurassic, some 160,000,000 years later. The highest mean rate of differentiation was about 6 genera per million years which was exceeded by both the trilobites and Foraminifera at their peak times. Judging from the fossil record, the belemnoids experienced an evolutionary peak at the same time as the ammonoids in the Jurassic.

Trilobita.—The trilobites (fig. 7) reach their acme in the period of introduction, the Cambrian, and they declined rapidly to a Silurian depression, followed by a minor peak in the Devonian, marking the rise and spread of the phacopids and a few other groups. The trilobites were at low ebb throughout the late Paleozoic so that their extinction at the close of the Permian, although not necessarily inevitable, was not an outstanding event of the time.

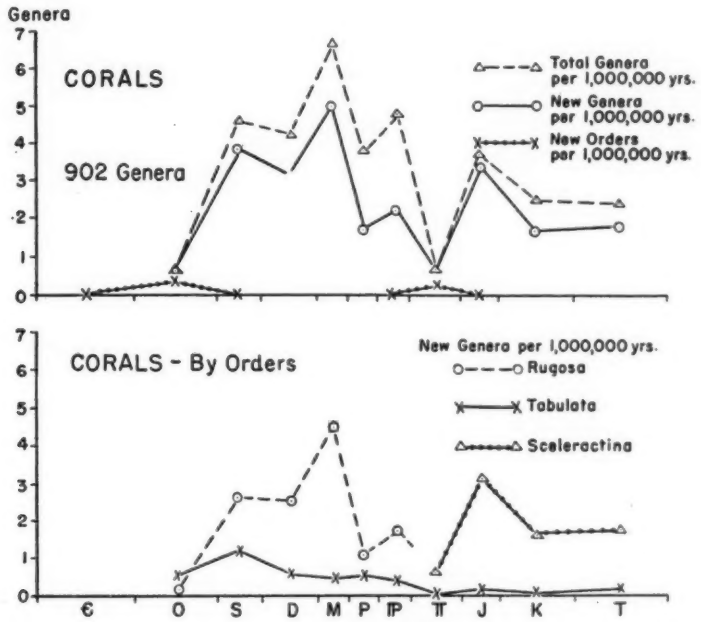

FIG. 3—Corals. Total number of genera and numbers of new genera per million years.

COMPETITION AND REPLACEMENT

Related animals generally have closely similar life requirements. As a result they tend to compete for those environmental factors where their needs overlap. Competition among invertebrates of the sea involves struggle for space in areas of optimum conditions of temperature, salinity, and food abundance, among others. Consequently, a common tendency here, as in other organisms, is for closely related animals to be-

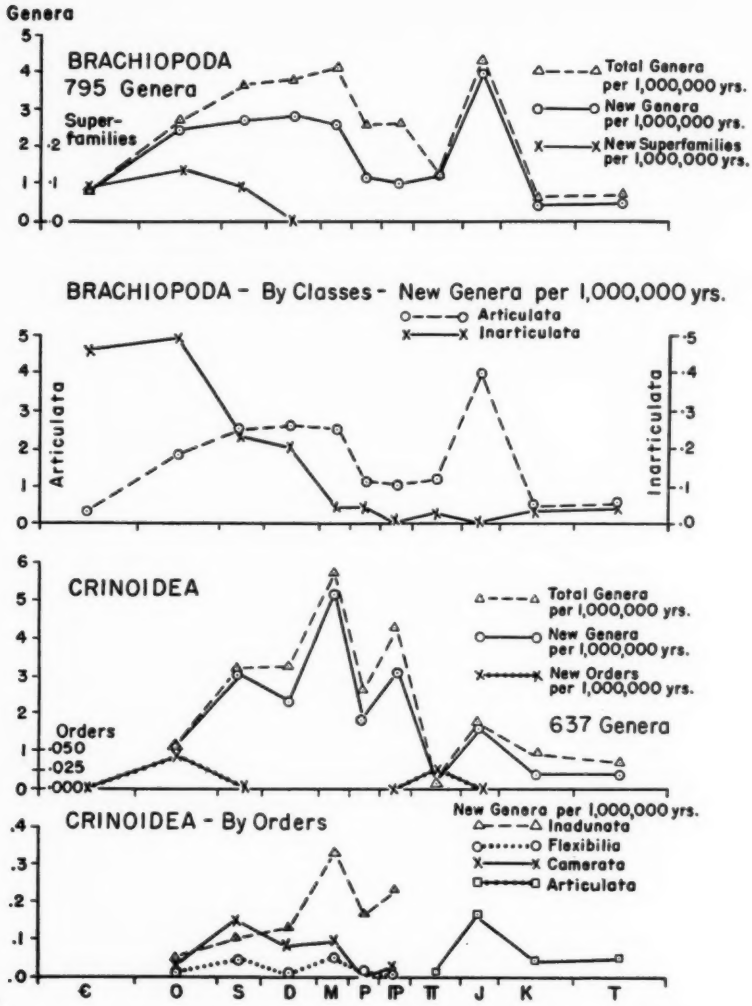

FIG. 4—Brachiopods and crinoids. Total number of genera and numbers of new genera per million years.

come adapted to slightly unlike ways of life, thus reducing unfavorable competition. It may happen, however, that a group gains an advantage over competitors by development of new structures or by perfection of old ones. The group so favored will tend to usurp the place of less well equipped animals. Possibly this is what happened to the nautiloids when the more active ammonoids appeared on the scene (fig. 6). The nautiloids appear to have declined steadily as the ammonoids became more diversified. It is possible, however, that the decline of the nautiloids was partly brought about by the rise of predaceous fish (fig. 7) which like the ammonoids became more diverse as the nautiloids declined. The trilobite record (fig. 7) also is a complement of the fish record in the sense that the trilobites diminished in variety as the fish expanded. Now, of course, this may be a fortuitous relationship, but it is highly probable that the trilobites, nautiloids, ammonoids and fishes did compete with each other, and the fishes certainly have gained ascendency over the others. It may well be that the decline of

the ammonites and belemnites after the Jurassic was partly related to the rise of the most advanced order of fishes, during the same interval.

As we have seen, the same mutually exclusive relationships mark the rise of the articulate brachiopods and the decline of the inarticulates. An animal group may be held in check by competitors until it can expand after competitors become extinct. This may account for the striking efflorescence of the cyclostome bryozoans in the Mesozoic (fig. 2) after a long and stagnant history in the Paleozoic. The Mesozoic rise in this group begins after the extinction of two other classes of bryozoans, which doubtless had been important factors in bryozoan competition.

Echinoids illustrate the principle of replacement of conservative groups by better equipped progressive groups. For instance, "regular" echinoids of the Paleozoic are characterized by comparatively weak, and in many cases, flexible sutures between the skeletal plates. In the Triassic there appeared types with relatively rigid and strong skeletons. This modification of the corona may well have been a factor in the great expansion of this group during the Jurassic (fig. 5). But a radically different adaptive type, the "irregular" echinoids, also first appear in the Upper Triassic. With superior defense and feeding mechanisms and stronger skeletons, these forms gained ascendency in the Cretaceous, and have retained it ever since. It may be that the rise of the irregular forms is in part responsible for the decline of the regular echinoids.

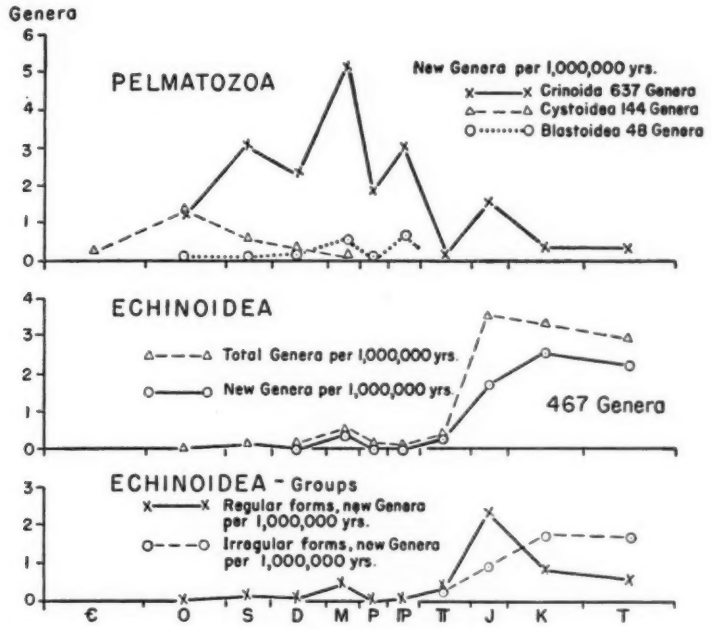
Genera
PELMATOZOA
New Genera per 1,000,000 yrs.
Crinoida 637 Genera
Cystoidea 144 Genera
Blastoidea 48 Genera
ECHINOIDEA
Total Genera per 1,000,000 yrs.
New Genera per 1,000,000 yrs.
467 Genera
ECHINOIDEA - Groups
Regular forms, new Genera per 1,000,000 yrs.
Irregular forms, new Genera per 1,000,000 yrs.
€ O S D M P IP Tr J K T

FIG. 5—Pelmatozoa and Echinoidea. Total number of genera and numbers of new genera per million years.

The blastoids show progressive replacement of the cystoids (fig. 5) and this may well have been a result of competition between them for an environmental niche. Reasons for extinction of the blastoids may be sought in the general late Paleozoic crisis. They reached their greatest diversity during the Permian, the period of extinction.

FLUCTUATIONS IN RATES OF EVOLUTION

We have seen that some of the major

groups of invertebrates exhibit successive peaks and depressions in evolutionary activity and that there is a tendency for many, but not all of them to rise to a peak of activity in the next period after their appearance. The question may now be put: To what extent do these fluctuations in different groups coincide in time? Graphs showing rates of generic differentiation are superposed (fig. 8) in such a way that the most similar patterns are grouped. The patterns of the corals and crinoids show identical distribution of highs and lows that can hardly be a chance correspondence. Likewise, the patterns of the ostracodes and bryozoans are nearly coincident throughout much of their history. The brachiopods, on the other hand, have a different pattern. The echinoids and forams show progressive increase in diversity over a tremendous span of time.

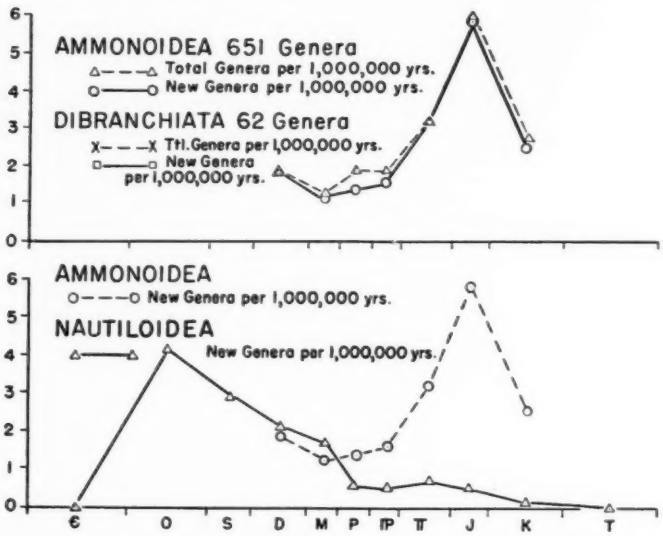
AMMONOIDEA 651 Genera
Total Genera per 1,000,000 yrs.
New Genera per 1,000,000 yrs.
DIBRANCHIATA 62 Genera
Ttl. Genera per 1,000,000 yrs.
New Genera per 1,000,000 yrs.
AMMONOIDEA
New Genera per 1,000,000 yrs.
NAUTILOIDEA
New Genera per 1,000,000 yrs.
0 1 2 3 4 5 6
Є O S D M P IP Tr J K T

FIG. 6—Cephalopoda. Total number of genera and numbers of new genera per million years.

Figure 9 synthesizes data from the preceding graphs. Here are shown the numbers of groups in peak stage for each period. In addition, the numbers of major groups first and last recorded in each period are shown. Salient periods of evolutionary activity are the Ordovician, Silurian, Mississippian, Permian and Jurassic. Of these the Silurian and Permian highs probably do not represent general eruptions above the level of families, but rather culminations of trends at constant or even relatively diminishing rates, as will be seen later (fig. 10). The Ordovician, Mississippian and Jurassic highs cannot be regarded as artifacts resulting from uneven paleontological discovery and study, or from favorable facies. Times of reduced activity and diversity are the Devonian, Pennsylvanian, Triassic and Tertiary. Ordinal and class extinctions are concentrated at the end of the Paleozoic era but are not confined to this part of the record.

The most pronounced slack period was the Pennsylvanian in which differentiation of new genera was at a low ebb. Rate of extinction, however, was not unusually high at this time. If the extinction rate had been high, it would have represented a crisis and the Pennsylvanian period might have come to be regarded as closing the Paleozoic.

Significant correspondence in the records of various groups of invertebrates is revealed when curves of the ratio of new to total genera are compared with the other records (fig. 10). Rise in these curves indicates an increasing proportion of new genera to survivors. A rise in this ratio is an essential aspect of eruptive evolution, as is

also an increase in the frequency with which new genera appear.

On the graphs of figure 11 are encircled those points where high production rates correspond to a relatively high percentage of low new/total ratios. The general climb in percentage of new genera after the post-Permian wholesale extinctions is abrupt and impressive. Because so few genera cross the Paleozoic-Mesozoic boundary, new gen-

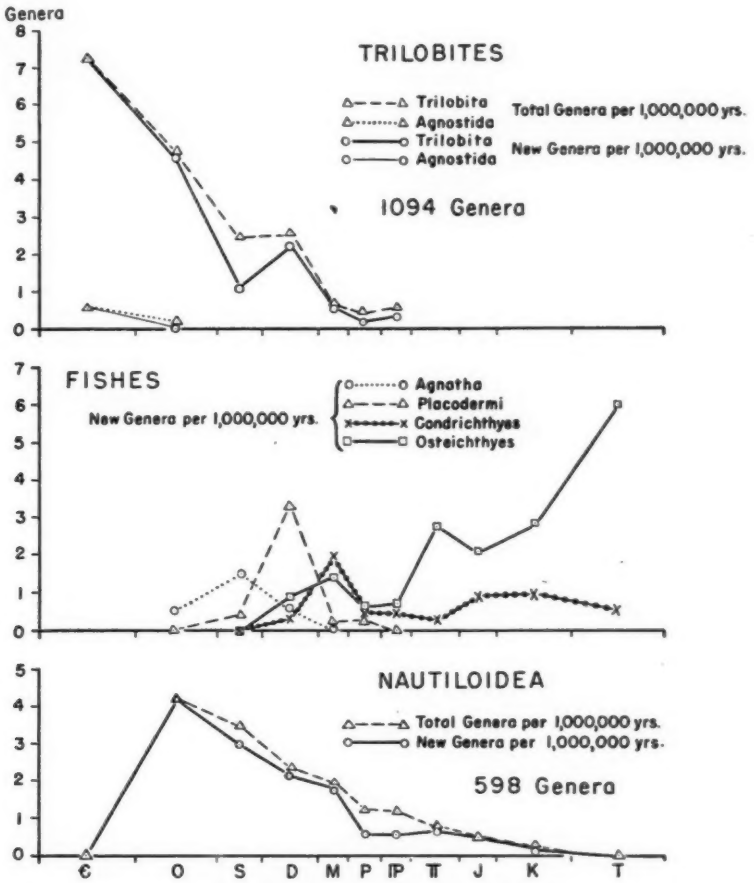

FIG. 7—Comparison of trilobites, nautiloids and fishes. Total number of genera and numbers of new genera per million years.

new genera. Three of the periods are outstanding as times of peak evolutionary activity. They are the Ordovician, Mississippian and Jurassic. One period, the Pennsylvanian, is unique in being populated by a relatively large proportion of genera surviving from the preceding period. Recovery from this Pennsylvanian slump was gradual in most groups. The depression extended into the Permian and in a few cases even into the Triassic, as shown by persistently era make up a very large proportion of the Triassic faunas, after which time survivors made up an increasing proportion of the total. The Triassic clearly initiated a time of eruptive evolution, but climaxes generally were not reached until the Jurassic.

Wholesale extinctions of major groups at the close of the Permian period in some ways mark the most critical time in invertebrate history since the early Cambrian. The Permian period was not a time of stagnation

comparable with the Pennsylvanian. In fact, it exceeded the Devonian, Pennsylvanian and Triassic in absolute rates at which new genera appeared, but the proportion of new genera in the faunas, as in the Pennsylvanian, was low.

The greatly reduced Triassic faunas reflect the depletion which resulted from the post-Permian crisis, in which the stagnation of the Pennsylvanian may have played a part. Early Triassic faunas the world over are extremely limited and unvaried. A number of major groups, which both before and after this time enjoyed noteworthy expansion, are conspicuously rare or absent in lower Triassic rocks. Bryozoa, corals, echinoids, crinoids, ostracodes and Foraminifera, among other groups, are scarcely known in the lower Triassic. But, nautiloids and ammonoids are well represented, and brachiopods, pelecypods and gastropods are common although not very diverse. Considering the Triassic as a whole, the faunas are dominated by the mollusks and otherwise are very limited in variety. This situation probably is a direct outcome of the wholesale decimation of the marine faunas at the close of the Permian, and certainly cannot be dismissed as an effect of "unfavorable facies." Initial variety was limited so that absolute rates of multiplication of genera were relatively low. The mollusks and echinoids show no appreciable decline at the close of the Permian, but rise steadily from a low point in the Pennsylvanian to highs in the Triassic period, sug-

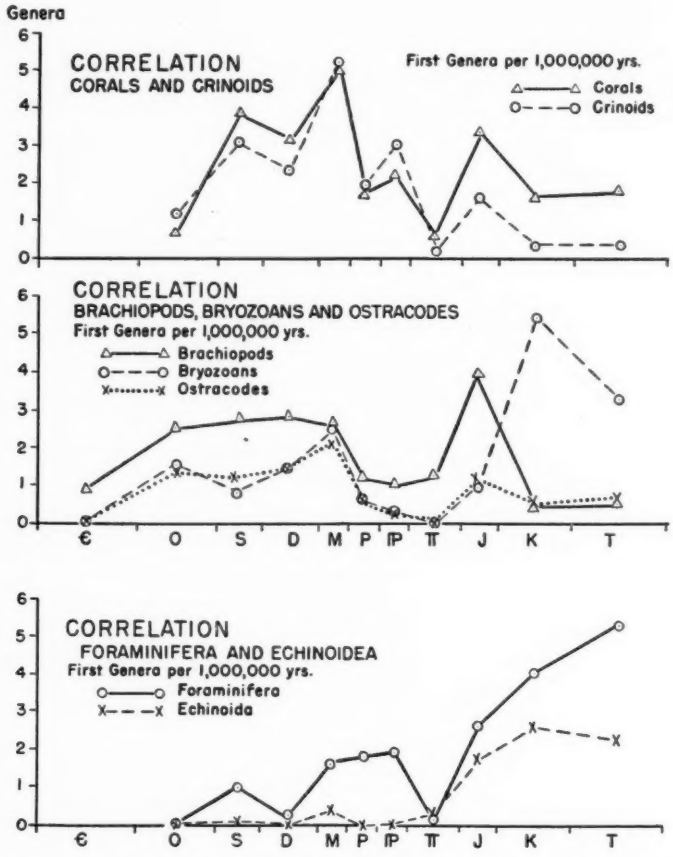

FIG. 8—Comparison of similar graphs and numbers of new genera per million years in several groups of invertebrates.

gesting that these groups were not affected by conditions at the close of the Permian to the extent of more sedentary groups.

OPPORTUNISM IN INVERTEBRATE EVOLUTION

There is little indication that the peak periods of generic differentiation in the Ordovician, Mississippian and Jurassic periods are directly related to orogenic cycles. In fact, the times of low activity as compared with the peaks fall in the Devonian, Pennsylvanian, Permian, Cretaceous and Tertiary, which often are considered to be times of exceptional diastrophic unrest. Nor is it likely that orogenic cycles inhibit evolution any more than they stimulate it. Environmental changes may affect evolution indirectly by causing extinction, migrations, destruction of old and formation of new habitats; but there is no evident reason for supposing that sweeping changes in physical environment can directly affect relative rates of evolution.

It may be helpful to regard the percentage of new genera in a fauna as a rough indication of the relative rate at which adaptational opportunities are realized. It seems fair to assume that many available habitats were unoccupied by marine invertebrates in the Cambrian and Triassic periods. Invertebrate life during the Cambrian was relatively undiversified as compared with later times. For a different reason a similar situation prevailed during the Triassic period. Ecologic niches dominated by various groups during the Paleozoic were vacated or were only sparsely occupied after the ex-

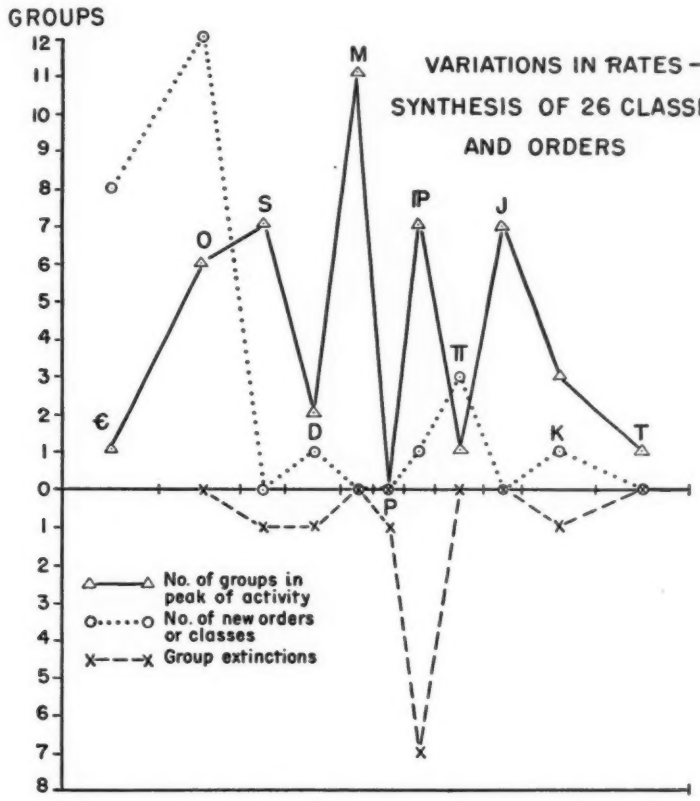

FIG. 9—Synthetic graph showing times of highest rates of generic differentiation, and times of first appearance and extinction of major groups of invertebrates.

tinctions at the end of the era. A sort of adaptational vacuum must have characterized these two periods. The result was high rates of differentiation, and of course, high percentages of new genera, approaching one hundred per cent.

With radiation of adaptive types at high rates during these periods, ecologic niches

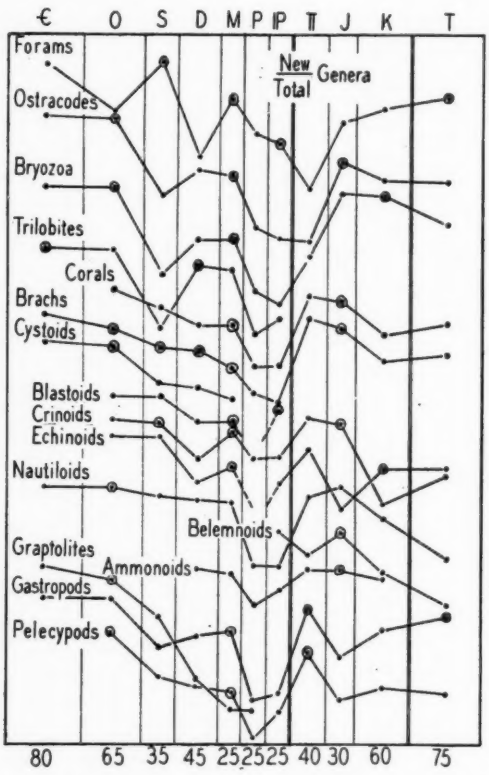

FIG. *10*—Synthetic graph showing comparative fluctuations in the percentage of new genera in successive faunas.

surely were modified and new niches brought into existence by the changing biologic elements. As every organism forms part of its niche, these Cambrian and Triassic animals made changes in their environments. However, ecologic niches certainly cannot be multiplied without limit, either by means of biologic or physical changes.

The relative numbers of accessible niches available probably decreased and those occupied became more crowded during the Cambrian and Ordovician, and again from the Triassic through the Jurassic. Both the Ordovician and Jurassic were times of culmination of eruptive trends which had originated in the preceding period. These trends reached a climax when relative equilibrium was reached. Opportunities in the form of unexploited or uncrowded major habitats became rare. Time required for the early Paleozoic burst was at least 110 million years, and for the early Mesozoic some 40 to 50 million years. Thus, the Ordovician and Jurassic peaks may simply be regarded as culminating times of radiation into an extraordinary number of available niches.

It is a well-known fact that the extinction of genera of marine invertebrates commonly is relatively great at the end of a geologic period. Many extinctions, of course, are an effect of evolution itself. As a genus evolves and passes into a descendent genus, we say that the older genus has become extinct, even though the lineage to which it belongs survives. Other genera drop out because the line to which they belong dies. The high rates of extinction at the close of a geologic era, period, or epoch, are most readily explainable in terms of withdrawal of the epicontinental seas from the continents. This change in the environment appears to me to be the only one capable of producing mass extinctions of marine genera on a global scale.

Judging from the data at hand, however, changes at the close of the Ordovician, and at the close of the Silurian, did not result in sweeping abandonment of ecologic niches through extinction. In some groups, for example, Foraminifera, crinoids, and corals, the early Paleozoic eruption did not reach a climax until the Silurian.

The slump culminating in the Devonian started in several groups immediately after the Ordovician peak, in a few others after a Silurian climax. In harmony with the theory of adaptive opportunism is it not probable that the interval from the Ordovician peak to the Devonian depression was characterized by gradual decline in environmental opportunities available to the then existing stocks? The relative extent of the marine withdrawal at the close of the Devonian is debatable, but there is no conclusive evi-

dence that it was a minor one. In any case increased rates of extinction in the Devonian, together with lowered rates of differentiation in several groups, may have opened the way for a Mississippian eruption. Simultaneous expansion of so many groups during the Mississippian suggests that far more opportunities for adaptation were available than in either the Devonian or Pennsylvanian. This may have been brought about by reduction of competition through Devonian extinctions, and it may have involved production of new habitats by means of vast environmental changes. A more satisfactory explanation does not now present itself.

The Pennsylvanian depression may in part be an effect of the Mississippian peak. Since the Pennsylvanian seas were populated largely by surviving genera, it appears that a condition of evolutionary equilibrium had been achieved in a majority of stocks. Perhaps available environmental niches were generally occupied to capacity. The balance continued into the Permian with only minor expansion in a few groups, but was upset by environmental changes at the close of the Permian when there was climactic depletion of existing genera.

Rise from the beginning of the Triassic to a Jurassic peak may be related to abundant new opportunities caused by the post-Paleozoic extinctions. Decline in rates of evolution from the Jurassic peak until the present, in most groups, is an expression of approximate equilibrium. This has been disturbed chiefly by gradual changes introduced by competition and replacement.

SUMMARY

Analyses of the better records of the fossil invertebrates show that rise and fall in apparent evolutionary activity is not at random. In a large proportion of the major groups, times of low evolutionary activity tend to coincide. This indicates a common external cause, namely, the relatively complete occupation of available and accessible habitats. This implies a sort of adaptational equilibrium. Any balance, or stagnation in evolution, of course is relative, and does not imply cessation or reduction in rates of mutation and selection. Indeed, a nearly static condition in evolution probably is caused by compensating high selection pressures leading to reduced variation.

The periods of relatively low average activity are followed by times of relatively high extinction rates. Principal of these were the Devonian, and especially the Permian period. Great subsidence in mean sea level is regarded here as the most probable cause of concurrent mass extinctions in numerous unrelated orders and classes. These times of wholesale extinction were followed by renewed radiation into vacant or uncrowded ecologic niches. The first of these widespread evolutionary expansions was during the Cambrian and Ordovician. The second, a minor burst, occupied the Mississippian. The third eruption, responsible for the general aspect of modern invertebrate faunas, occurred in the Triassic and Jurassic.

The major fluctuations in invertebrate evolution, then, appear to have a physical basis in submarine diastrophism, but the relationship is an indirect one by way of extinction. In all probability, the fluctuations in evolutionary activity are not directly related to times of widespread orogeny, and there is no indication that peak times of evolutionary activity correspond with times of extensive orogeny.

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DISCUSSION[1]

WENDELL WOODRING, *Chairman*

M. K. ELIAS (University of Nebraska, Lincoln): I find it difficult to discuss this symposium because of the diversity and number of interesting points raised. But I have picked out at random certain things that struck me rather forcibly as being at variance with some fundamentals in paleontology. . . .

I am shocked by the use of the sensational term "explosion." If we only realized the tremendous time that is involved in this seeming "explosion" we would see that in the proper perspective the phenomena of apparent evolution are extremely small. As an illustration: Julian Huxley, as I recall, estimated that the fruit fly *Drosophila* under experimental conditions, in which it constitutes an example of most rapid or "explosive" evolution, could be expected to produce a new species in about 3,000 years. Now, if you just compare this 3,000 years time with the rate of species produced the fastest in geologic time, you will see that this so-called explosive evolution is really far slower than it seems. I don't think we have such a thing as explosive evolution. It is a product of our imagination.

One of the very able speakers indicated that crinoids in their evolution occur in great number of genera and species in the middle of a period of time, and then their number dwindles at the end of the period, and then the next peak is reached in the middle of the next period of time, and so on. But as geologists we must remember that the sediments available for our study always decrease at the end of each period of time, and then they begin to increase, as the seas of the next period of time begin to expand. The absence or scarcity of sediments at the beginning or end of each period of time accounts very easily for the decrease of the known genera and species of these times. So how can we speak about a certain explosion reaching a peak and dwindling? It is really not based on substantial paleontological facts at all. . . .

CARL O. DUNBAR (Yale University, New Haven, Connecticut): This has been a thoroughly stimulating symposium, and most of us probably find our minds at this moment grappling with conflicting ideas that struggle for evaluation. Time will be required to assimilate the array of facts so ably presented by many speakers. I shall therefore limit my discussion to brief comment on two points.

First, it was the purpose of the symposium, I take it, to challenge those extremists who believe that orogenic episodes provide a natural basis for the major subdivisions of geologic time, and many of the lances raised today have been directed at that narrow view. Throughout most of the discussion, however, the terms orogeny and diastrophism have been used almost indiscriminately as though they were synonymous. It would be better, I think, to keep clear the distinction between two aspects of diastrophism. Orogeny is essentially local and may be relatively transient, but is marked by an impressive display of force; epeirogeny, on the contrary, includes those vast but gentler movements that alternately raise and depress large parts of the continental masses, negative movements permitting widespread accumulation of stratigraphic record on the continents whereas positive movements cause the loss

[1] The following account of the Discussion represents the substance but not necessarily a rigidly verbatim record of the addresses which were extempore. The stenographic record was sent to the participants who were given opportunity to make corrections and to clarify their remarks within the substance of the original. Throughout the program, various amenities and incidental remarks by the speakers and by the Chairmen represented definite contributions to the success of the symposium, but as these were not material to the published discourse they were omitted.—L.G.H.

of record into the ocean basins. Whether such movements are synchronous in different parts of the world to a degree that provides a natural basis for geologic systems cannot be surely known until paleogeographic data are compiled on a global scale; but epeirogeny now appears far more likely to provide a natural basis for geologic classification than does orogeny, and it is worth noting that the pulse of life may be synchronized with epeirogenic rather than orogenic changes.

My second point concerns the seemingly contradictory conclusion reached by Dr. Simpson and Dr. Newell on the one hand and by Dr. Cooper and Dr. Moore on the other. The first two have analyzed the paleontological record of several classes of animals by determining the *number* of families and of genera known for each in successive periods. Their simple curves show clearly the basic pattern of the rise and decline of the larger groups of organisms in which neither the time of origin, of climax, or of decline shows any obvious relation to systemic boundaries or to times of notable orogeny, save for the remarkable coincidence of changes near the close of the Paleozoic era.

Drs. Cooper and Moore have analyzed the record in much greater detail, counting the families in each order and the genera in each family in each *series* of each geologic system, and have represented the history of each small biologic unit as a line whose width varies with its importance. When treated thus the record is seen to be nodal, and marked changes coincide mostly with systemic or series boundaries. Even though the total number of genera in a class may rise somewhat from one period to the next, detailed analysis shows that they are mostly different genera and even different families that have arisen or have rapidly expanded to replace others that have dropped out at the end of a period. If there be examples of *explosive* evolution, they are to be found here in the genera and families of organisms rather than in classes and phyla.

Whatever the actual course of evolution may have been, the known record cannot be represented as a smooth flowing curve. In part the nodes in the diagrams presented by Drs. Cooper and Moore are due to unequal monographic studies but in large part they are due to breaks in the record. And whether such breaks are actual hiatuses or merely widespread unsuitable facies, they stem from diastrophic changes in the Earth. It is improbable, for example, that life on Earth was greatly restricted during late Silurian time, but we have yet to find a richly fossiliferous marine record comparable to that of the Middle Silurian or of Early Devonian. Debate as to whether evolution is greatly stimulated by such physical changes should not obscure the fact that presently recognized systemic boundaries coincide with many important changes in the organic record.

The analyses graphically presented by Drs. Simpson and Newell do not really contradict those presented by Drs. Cooper and Moore; they simply represent different aspects of the complex history of life.

JAMES STEELE WILLIAMS (U. S. Geological Survey, Washington, D. C.): The evidence for evolutionary explosions depends, in many instances, on the accuracy of detailed stratigraphic correlations.

In my opinion paleontologists have fallen into a way of thinking that greatly undervalues the roles of ecology and geography in determining the ranges of species and genera and the compositions of faunas. That ecologic conditions do influence these things has been known for a long time, and this fact is in the back of the mind of every experienced paleontologist. Yet, in practice, it is often assumed that the faunas of very thin zones, characteristic of certain regions where alternations in sedimentation were unusually frequent, must each be recognizable and distinct the world over, even in basins where sedimentation of one general type was more or less continuous for a long time. Much of this thinking and the detailed correlations that follow it are based on the assumed infallibility of a few so-called index fossils. Often the individual paleontologist making such correlations relies almost entirely on the single class of fossils about which he is best informed. To me these attempted world-wide correlations of thin zones suggest allegiance, perhaps unconscious, to two hypotheses long repudiated—the universal formations of Werner and the successive cataclysms of Cuvier.

Every index fossil, should, if my experience is any criterion, be suspect and its validity continually checked by evidence from other faunal data of several classes. It is not original to say so, but I believe it needs repeating that faunas of different basins differ; that they are influenced by local ecologic conditions; that some elements in them require time, even when time is measured in the geologic sense, to migrate from one basin to another; and that each year some so-called index fossils are found associated with older or younger faunas in different basins. The broad outlines of stratigraphy throughout most of the world have been well worked out by reference to adequate and varied paleontologic data. The details are more complex. Each basin or geographic region has its own lithologic and faunal peculiarities. Detailed data are available for only a few basins. Until such data of several types are available in many more of the individual basins, it seems premature to attach any reliability to many of the detailed correlations of thin zones between basins, especially between basins that are widely separated. I am speaking primarily of rocks and faunas of late Paleozoic age, for these are the ones with which I am most familiar.[2]

RAYMOND C. MOORE (University of Kansas, Lawrence, Kansas): I wish to respond to the remarks just made.

The seas have advanced over various continents simultaneously as indicated in many quarters and in many parts of the column. It is unreasonable, remembering Cuvier, remembering Werner, remembering Smith, to think that these transgressions, as in the Ordovician, the Silurian, the Mississippian, the Cretaceous are offset, as the fossils plainly say they were not. Granted that most organisms are affected by their environment, it still is true that the basic relations of the fossils and the rocks are the framework on which our whole stratigraphy over the world is based.

Studying genera of the crinoids brings out the same essential picture, although with certain smoothing of curves that the species indicate. And I think one reason for the great expansions, which are recorded on the different sides of the oceans, is that the seas which brought favorable living conditions to these crinoids were wide spread in those parts of the geologic succession shown.

P. E. CLOUD, JR. (U. S. Geological Survey, Washington, D. C.): Speculation about causes for times of seemingly abrupt appearance of new morphologic grades, marked increase in taxonomic diversification, or great preponderance of certain species (in given areas) calls for consideration of important ecologic factors.

It is generally true among Recent faunas that where a large variety of species occurs in any given area, the number of individuals of each species is prone to be relatively small, but where few species comprise a fauna, the number of individuals of each species is likely to be large. It is also true that populations of species wherein individuals are large are generally less numerous than populations of species made up of small individuals. The total volume of animal life that can exist at any place is limited by the supply of primary vegetal nutrient available, as well as by other factors. Assuming adequate food supply, the total volume of life at any place may consist of relatively large populations of a small variety of species of small individuals, smaller populations of a larger number of species of small individuals, or even smaller populations of large individuals. Ordinarily both species comprised of large individuals and species comprised of small individuals are present.

The variety of Recent animal life within any particular area is related to the variety of ecologic niches available for habitation. The variety is thus also related eventually to the various physical factors (including nonorganic chemical, and geographic) that go to define separate ecologic niches and to determine what manner of life may survive in them. Of the complex of factors that control the existence of a particular species and its persistence at any given place, primary limitation is exercised by that factor for which that species has the narrowest range of adaptability. The more nearly any single factor approximates a general limiting value over any given area, the fewer the number of species that can inhabit that area.

[2] Published with the approval of the Director, United States Geological Survey.

Ecologists call this the "law of the minimum" or "principle of the minimum," initially formulated in more limited terms by the botanist Liebig.[3] The principle of the minimum perhaps explains why specific variation is greater and individual populations smaller in tropic than in arctic and subarctic environments (other than deserts). In order for a species to continue to inhabit any given ecologic niche it must be able to live all year round in some form and be viable at all developmental stages—and a greater variety of species can do this in the uniform climate of the tropics than under the climatic stresses of far northern areas. It is doubtful whether there is a significantly wider variety of primary nonorganic ecologic diversification in tropical than in northern realms, but ultimately, because of climatically limited organic complexes such as coral reefs and tropical rainforests the actual number of available ecologic niches is greater.

The principle of the minimum affects the subject of this symposium in another way. The point has been raised that inasmuch as physical factors should affect all life within the region of their application, eruptive evolution, if influenced by major physical changes, should occur concomitantly in all groups within the realm and region of their application. But there are doubtless some and perhaps many instances where the same physical changes that permitted certain groups to expand and diversify affected other groups restrictively through factors of minimum adaptiveness. Such restriction amounts to selective pressure, and it is selective pressure that keeps evolution channeled in patterns of slight diversity.

Factors that determine abundance and variety of animal life would appear to be (1) supply of nutrients, relating to the physical factor of penetration, duration, and obliquity of sunlight providing for the basic nutrient factor of plant life through photosynthesis, (2) variety of ecologic niches, primarily determined by physical factors, and (3) the principle of the minimum. Operating through these limiting factors and the genetic composition of the faunas affected, natural selection will control the survival patterns.

Fairly reasonable explanations for the types of "eruptions" or "bursts" of animal life that have been mentioned today may be formulated. (1) Occurrences of natural assemblages of large numbers of individuals of few species (not due to sorting after death) are probably related to "minimum" factors that permitted only relatively small numbers of species to live in situations of abundant primary nutrient supply. (2) Eruptive evolution of great taxonomic variety may well find its explanation in great diversity of available ecologic niches combined with other factors such as relaxation of selective pressure or onset of paedomorphic tendencies (early ontogenetic changes, affecting later growth stages). And (3) abrupt appearance of new morphologic grades is probably related to the factors suggested as influential in production of great taxonomic variety, with possible emphasis on paedomorphic tendencies.

Possibly in any given major group of animals an eruption of new morphologic grades (type 3) will ordinarily precede an eruption of the type that produces great variety in lesser taxonomic ranks (type 2), setting the scene, as it were, for the latter development in a following period of marked ecologic diversity. The mere occurrence of large numbers of individuals of one or several species (type 1) is not to be regarded as eruptive or "explosive" in the sense that the expression is most commonly used.

I should like to maintain that times of eruptive evolution may well be, in fact probably are, related to important events in the physical history of the earth.[4] It is, of course, not a new idea to suggest that times of high stand of the continents and restricted epicontinental seas were probably times of climatic extremes, and, as regards marine invertebrates, times of reduced ecologic diversity and increased competition for available niches, generally productive of channeled evolutionary patterns. Following such times, wide inundation of the continents, producing a variety of ecologic

[3] LIEBIG, JUSTUS, 1840, Chemistry in its application to agriculture and physiology: London, Taylor and Walton.
ALLEE, W. C., et al., 1949, Principles of animal ecology: p. 198, 635; W. B. Saunders Co., Philadelphia and London.

[4] CLOUD, P. E., JR., 1948, Evolution, vol. 2, no. 4, pp. 342–349.

situations suitable for marine invertebrates and probably also ameliorating climatic conditions and generally reducing selective pressures, should be conducive to eruptive expansion. The reverse would generally apply to terrestrial biotas. There are other ways of producing ecologic diversity, of course, and the breadth of ancient seas did not necessarily have a controlling relationship to the degree of such diversity. Topography of the inundated landmass, complexity and type of marine ingress, and causes of inundation should have important effects.

It should hardly be necessary to argue that important changes between sea and land need not necessarily have been related to periods of marked or world-wide orogenesis. Any of various well-known factors that might affect the total volume of the ocean basins could have as important and more extensive effects than orogenesis, and epeirogenetic movements of land areas of subcontinental dimensions might have extensive effects without leaving marked physical evidences of their occurrence.

The point to keep in mind, I think, is that there are a variety of physical bases other than orogeny, or even diastrophism in broader terms, that could well be related to major episodes of organic evolution. It would be as regrettable at this turn to reject categorically the likelihood of cause-and-effect relationships between biological and physical evolution as it would be to insist that evolutionary bursts and diastrophism were synchronized in time.[5]

KIRTLEY MATHER (Harvard University, Cambridge, Massachusetts): I want to express, on behalf of all of us who are interested in getting a broad view of the overall picture of the history of the earth and its inhabitants, our very deep appreciation to those who have brought together in this synthetic form so many separate fragments of the jigsaw puzzle. This has been a most stimulating symposium for me, and I assume, therefore, for many others. Out of it I get some verifications of certain suspicions that I have had in the past. That, of course, is always a gratifying experience for a listener, Or, to put it another way, we have had here the quantitative verification of certain rather vague qualitative ideas that have been in our minds.

I am well aware of the fact that the figures that have been used are woefully inadequate to present the realities of life. There are so many factors that weight the figures one way or the other and cause them to move far away from the real facts. The accident of exposure of certain kinds of rocks in certain areas as a result of geologic history; the accident of personal commitment and interest; both result in the fact that some groups have been studied in some areas much more completely than other groups in the same area or in other areas. But is it not true that we have had here a demonstration of two or three rather important fundamental principles?

In the first place, the available evidence seems to indicate that there are no world-wide revolutions, either of a diastrophic nature or in the organic kingdom. Things are not happening through a series of revolutions. Instead we are observing the results of processes of evolution.

At times evolution operates more swiftly than at other times; or at least the results seem to be secured in briefer intervals than in other times. But the moments of rapid evolution—and I would much prefer that to the term "explosive evolution"—have occurred for different groups of animals, presumably also for different groups of plants, at different times. The movements of the earth, with innumerable consequences respecting many diverse environmental factors, have similarly been spaced out in an irregular manner. Environments have changed much more rapidly at certain times than at other times. But even when the environmental changes were most rapid it was not a revolution. It was still merely evolution.

Why there should be more speedy changes among any particular group of creatures at certain times than at others is still an unanswered question. One general conclusion has however appeared, or has been fortified by the quantitative data that have been used in these presentations. That is the general principle that the results of dias-

[5] Publication authorized by the Director, U. S. Geological Survey.

trophism, as it caused changes in the physical environments, must be considered as only one of the many causes for the changes in the rate of organic evolution. Surely, the other factors which we put together under the broad term of ecology must be rated as having nearly, if not quite as great significance as changes in the physical environment, important though the results of those changes may be.

I would compliment those who have participated in the symposium upon the results that they have brought to our attention here. We are making progress. But I am sure that all the paleontologists agree that we have still a long way to go. Many more analyses must be made, many more discrete facts must be brought to our attention before we can achieve a synthesis that has as much meaning as we would like to see. This symposium has, however, brought to our attention some very fundamental principles. I would sum them all up by repeating my assertion that we have been listening to descriptions of evolutionary rather than revolutionary changes in nature.

PARKER D. TRASK (Berkeley, California): It seems to me this afternoon we have seen an objective approach to evolution, and I don't see how we can escape from the statistical data that have been presented that we have certain evolutionary trends in different types of organisms going on at different rates and at different times. Now, I think you can challenge here and there, the idea that these rates are qualitative, not of the proper order of magnitude, but the general picture, I think, time will show will be substantially as has been presented.

However, I think there is one step further, which undoubtedly occurred to the speakers, particularly the last two speakers, that these evolutionary trends need to be correlated with some sort of physical factors which undoubtedly must have had something to do with those evolutionary trends, and some sort of a quantitative approach to these evolutionary factors must be attempted. We must have some quantitative evaluation of environment, or some of the principal factors of environment, such as rate of diastrophism, rate of sedimentation, and if we can study these quantitative evolutionary trends with respect to quantitative factors of environment, which is a very difficult thing, I think we can come to a clearer understanding.

It seems to me that when we say that diastrophism is or is not a factor in evolution, that is more or less, to my mind, a matter of opinion. We have not seen, at least in the last few papers which I heard—I did not come here at the beginning—we have not seen a quantitative approach to these factors of evolution through the physical factors. . . .

SIEMON WM. MULLER (Stanford University, Stanford, California): I should like to remark on one aspect of the discussion which has a bearing on the use of evolutionary changes in organisms—the use which we call the correlation of rocks—the establishing of the synchronization of strata.

In the first paper, which we heard this afternoon, it was brought out that the correlation of rocks may be regarded as chronologic or homotaxial. I wish to dwell for a moment on this concept of homotaxis.

In introducing the concept of homotaxis, Huxley had rightly challenged geologists to a claim that rocks in distant areas containing the same fossils are necessarily of exactly the same age.

I shall first make a qualifying statement that in my discussion of homotaxis I shall confine myself to the consideration of Paleozoic and Mesozoic strata which represent a very much greater span of time than the later geologic divisions, Tertiary and Quaternary, in which the relationship of the thicknesses of strata to their span of time is quite different.

One has a right to question that homotaxis as a concrete measurable entity does exist.

I should like to offer for your consideration a condition which appears to show that if homotaxis does exist, the magnitude of time which the organisms take to migrate from place to place is so small that it cannot be measured, and therefore for all practical purposes can be neglected.

I should like to cite a concrete example. Many of you are familiar with a rock unit locally known as the Caney shale, the Moorefield shale, the Barnett shale and which in

the West is called the White Pine shale. Within a narrow stratigraphic range this formation contains the following assemblage of organisms:

American Forms	European Equivalents
Goniatites choctawensis Shumard	= *G. crenistria* Phillips
Orthoceras sp.	= *O.* sp.
Aviculopecten catactus Meek	= *A. murchisoni* McCoy
Caneyella vaughani Girty and others.	= *Posidonia becheri* Bronn

Goniatites with a *Nautilus*-like shell was undoubtedly a free swimmer. *Orthoceras*, a primitive cephalopod, is generally regarded as a bottom dweller and was perhaps sluggish in his effort to "get around." The small, thin-shelled pecten, *Aviculopecten catactus* has a byssal notch which suggests that this organism, during a part or all of its life, was attached perhaps to a kelp. The thin-shelled pelecypod, *Posidonia becheri*, probably did not differ much in its habit from that of a pecten. Here we have then four different organisms with different capacities or rates of travel in their migration from one region to another. It is also reasonable to assume that the duration of the free swimming larval stage of each organism was different.

If all these organisms migrated from one area to another, and I don't mean a limited travel from Oklahoma to California, but in their long journey from Western Europe to North America (or vice versa), there surely ought to be some indication of a lag in the arrival at the destination on the part of the slow moving individuals.

The fact is that we find all these organisms in the same association in such widely separated areas as Belgium, Nevada, Oklahoma, Texas, and so on. The point is that there is no adequate means for detecting in terms of strata the element of time involved in the migration of these forms.

It has been pointed out by Dr. Spath of the British Museum (Natural History) that the ammonite assemblages are remarkably similar when they are strictly contemporaneous, wherever they occur. This conclusion is well substantiated by the occurrence in the Triassic rocks of Nevada of ammonite and pelecypod faunas which contain species identical to those which are found in similar assemblages in the Alps.

The facts presented above challenge the practical validity of the concept of homotaxis. In theory, and to conform to the logic, we must admit that it takes time for an organism to migrate from one area to another but in actual practice this time element in the pre-Cenozoic chapters of the Earth's history is so small in proportion to the stratal record, that it does not lend itself to be recognized or measured. Homotaxis as a philosophical concept cannot be denied but its application in the correlation of strata cannot be accepted unless it is backed by adequate evidence.

J. Brookes Knight (U. S. National Museum, Washington, D. C.): With reference to the speed with which a marine invertebrate can migrate where there is no barrier, we have an example in historic times on the North Atlantic coast of North America. As I recall, the gastropod *Littorina littorea* (Linné) was introduced accidentally from Europe around 1875. In about 25 years, it spread in abundance as far south as New York, the southern limit of the rocky coast to which it is adapted. In terms of geologic time this is practically instantaneous.

John Putnam Marble (U. S. National Museum, Washington, D. C.): The various paleontological speakers this afternoon have paid me and my colleagues on the Committee on Measurement of Geologic Time a very great compliment by putting millions of years as one of the coordinates in almost every one of their graphs, and I wish to express my deep gratitude for their belief in the data we present.

However, I think it might be well to point out just about how many absolute age determinations we have within the boundaries of the paleontologic column, running from the Pleistocene down to the bottom of the Cambrian, that fulfill to a considerable extent the six criteria that I set up as being among the ones that are important. They are very, very few. There is one in the Tertiary. There is absolutely nothing in the Mesozoic. The only Mesozoic determination we have is based on very

fragmentary evidence, and not enough material has turned up to enable us to improve its precision. We have two that apparently belong toward the end of the Paleozoic—whether Permo-Carboniferous or Pennsylvanian is still a matter of fervent debate. We have about three in the middle to older Paleozoic, and we have one in the Cambrian, and that one in the Cambrian is the only case where the radioactive stratigraphic column and the paleontologic stratigraphic column coincide. That is the famous Kölm of Westergotland in Sweden where the material containing the radioactive elements also contains recognizable fossils.

Now, from my recollection of the discussion that has been going on for many years in connection with the position of this material in the geologic column is that the fossils are reasonably diagnostic of Upper Cambrian but have a pretty wide range. I know from my own experience with the chemical and physical end of the work that the chemical and physical evidence for the exact age, in terms of years, for that particular occurrence, is not quite as good as some of the others. But the amount of work that has been done has all been done by competent men, and they, none of them, feel that they can improve the precision of that result which has probably a plus or minus error of 12 million years.

For further discussion of the position of these dates by radiogenic lead in the stratigraphic column, see Adolf Knopf's "Time in earth history."[6]

J. WYATT DURHAM (University of California, Berkeley, California): I am not at all sure the comments I have to make are pertinent to the previous discussion to the fullest extent, but they concern somewhat what might be called the perfidy of the fossil record. We have seen a number of graphs—I am referring now specifically to the marine invertebrates rather than the terrestrial organisms—recording the abundance of them, either in terms of percentage or actual abundance.

[6] Knopf, A., 1949, Time in earth history (in Jepsen, G. L., Simpson, G. G., and Mayr, E., Genetics, paleontology, and evolution): Princeton University Press, Princeton, N. J.

The first thing I would call your attention to is the fact that we are relatively unacquainted with the fossil-bearing rocks of a large part of the world, specifically, most of the land areas surrounding the Pacific Basin. Much of South America is unknown paleontologically. Most of eastern Asia is in the same category. To emphasize that particular point, I call attention to the Permian and Triassic of the Dutch East Indies. If you will notice, on several of the graphs represented a low number of genera leading up to the Permian, and then all of a sudden in the Permian a high point was shown. That high point was due to the wonderful assemblages that were found in the Permian of the Island of Timor. Those exposures are not very extensive, and if we should have a sudden diastrophic movement out there, all those sediments might go beneath the sea; or if we had a big volcanic explosion they might disappear, and then the evidence for that high point, if someone hadn't already recorded it, would have disappeared.

I call attention, furthermore, to one of the graphs of Dr. Moore. In Tertiary he had a record—a little point, not a very big one this time—but nevertheless a record of crinoid genera. It is due to fossils collected from a particular exposure in the state of Oregon. The uniqueness of the fauna from this locality was not known until very recently. I imagine that at the time he compiled that graph he knew only that crinoids occurred there. I visited that exposure last summer. We collected from this exposure a great many specimens of a coral that had previously been known by only three individuals from other localities. We collected a whole host of individuals of an echinoid as yet unidentified. We collected at least three genera of star fish. There are also a number of genera of mollusks that have not been recorded previously as fossils. In all, the fauna from this particular locality is so notable that it will decidedly influence the known Tertiary record of many groups of organisms. That is one point.

I would call attention to another experience of my own. I thought I had a very wonderful discovery a year ago. Dr. Harold E. Vokes had sent me a coral for examination. I looked at it and saw immediately it

was a very unusual genus, hard to confuse with any other, which had been known previously only from the Paleocene of the London basin. Here it occurs in Oregon, but as I found out later it was from strata of upper Eocene age instead of Paleocene. Where is the rest of the fossil record of this coral?

One other point. A statement is found in the literature in a number of places to the effect that the coral fauna—I am speaking now of the Recent coral fauna of the eastern Pacific—is very scanty. I have had occasion to be connected with two different studies of this fauna, and even the one now in progress is not based on adequate collections of Recent material. Yet in these two studies we have had occasion to enlarge the known coral fauna, the living coral fauna of the eastern Pacific, to about double the number of genera and species previously known. The same thing has occurred in the fossil corals of the Pacific Coast Tertiary. Through no virtue of my own, I happen to be the main one working in that field, But since I have been working in that field, I have turned up four times the number of genera that were previously known, and a proportionately greater number of species.

Finally three years ago one of my students turned up some fossil star fish in the Cretaceous of southern California. He and I described them, and I made a summary of all the records of fossil star fish in North America, from the Jurassic through the Tertiary. I think the total was something in the neighborhood of 15 records. Since that time, five different occurrences of fossil star fish in the Tertiary and upper Cretaceous of the Pacific Coast have turned up, and they involve about six different genera. If those discoveries were plotted on a percentage basis for the fossil star fish, they would make a big change in the abundance curve in the past three years as compared to that of previous years.

P. E. CLOUD, JR. (U. S. Geological Survey, Washington, D. C.): If I may have your second indulgence there is another point of philosophy that I meant to bring out earlier, a point not in the main original but I think important.

Dr. Camp noted in his discussion that times of evolutionary bursts among vertebrates did not fall in line very well with stratigraphic boundaries as presently recognized. This may be explained by the fact that, for reasons well known to all, stratigraphic boundaries are based primarily on changes in marine invertebrate faunas, while major physical effects probably tend to affect marine and continental biotas in generally opposite ways.

Maximum continental inundation should produce a wide variety of ecologic niches for diversification of marine invertebrates with a minimum diversity of ecologic situations for terrestrial faunas to evolve into; whereas the reverse might well be true for times of maximum continental emergence.

Similarly barriers have quite different effects in relation to marine and continental biotas. The presence or absence of an isthmus between North and South America for instance would tend to have exactly opposite effects as related to isolation or intermingling of marine and terrestrial life.[5]

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TRIASSIC REPTILIAN TRACKS AND TRENDS OF LOCOMOTIVE EVOLUTION

WITH REMARKS ON CORRELATION

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ABSTRACT—The bearing of the mechanical principles of locomotion on the evidence of fossil reptile tracks is pointed out, and the evolution of tetrapod locomotion, including several components of motion, is discussed. The pendulum limb movement and the roll-off functions are considered. New reptilian foot-prints from Upper Triassic formations of eastern Pennsylvania are described, including the track of four species of *Chirotherium*, six saurischians, three small pseudosuchians, one cotylosaurian and two lacertoid-like forms. A map of the area is added, correlating the Triassic formations of this part of the Newark Basin, the Stockton, Lockatong and Brunswick formations, with the equivalent European formations, extending from the Schilfsandstein up to the Knollenmergel, which practically comprises the whole middle Keuper.

INTRODUCTION

ACCORDING to the rigid concepts of the paleo-osteologist it may not always appear convincing that a knowledge of the mechanical principles of biological locomotion is an aid in working out classification of vertebrate fossils. Fossil tracks are often only reluctantly accepted as prima facie evidence in this field, although they are frequently a source of much information. If we remember that a working horse may produce more than 10,000 tracks a day and continue to do so for 20 years, the resulting million or so imprints make us realize that the animal has made an impressive record. But when we find a single fossil footprint, or a few fossil tracks, we may deduce, from simple mathematical probabilities, that the chance of securing the bones of the animal which made them is indeed slim. To underestimate the importance of track evidence in the over-all picture of our prehistoric world, however, will merely delay closing some of the many remaining evolutionary gaps. Moreover, good imprints not only preserve anatomical and surface forms, but also disclose records of actual motor functions of the vanished creature, which shed much light on the basic locomotive operations and the structure of the body. Soergel (1925) was able to reconstruct, as a classical piece of dynamic paleontology, the body form of the still elusive large European Triassic reptile, *Chirotherium*, from many functional details of its tracks. The unchallenged acceptance of his conclusions can be considered a proof of the soundness of his findings. Doubtless the basic mechanical details of locomotion remain an inseparable part of ichnology. It is hoped that the present paper will add also to our knowledge of the Triassic reptiles of the eastern United States.

EVOLUTIONARY TRENDS OF THE MECHANICS OF TETRAPOD LOCOMOTION

One important lesson which paleontology has taught is that the development of biological processes is a secondary phenomenon. These processes are largely the result of the smooth team work of two integral agencies of energy, gravitational and thermal forces, without which biological records could not continue. Thus, physical laws fundamentally control all elements of evolution, and its form and expression are shaped by them. The directing power, which man is only permitted to suspect, is as untouchable as the "Ding an sich" of Kant, and we should only lose ourselves in trying to approach it with our limited means of recognizing physical variations.

Of the two main forces cited, it may be difficult to decide which is the controlling factor; but one must not lose sight of the geological fact that gravitational energy primarily accumulated the media of water and air in successive stages of temperature

changes, in which surroundings only could biological growth occur. Whatever, and however small, the first expression of biological processes may have been, the influence of gravitation on it has been essential. Nearly all growth has been directed along its vector forces.

The basic development of a functional biological course, to synchronize properly with the force of terrestrial attraction, requires confinement of the matter involved in a vessel, or container, of any suitable shape, but not hermetically closed, in which it can direct and concentrate its vital thermal and metabolic operations without being dispersed by the gravitational vector forces. Any biological substance, whatever the shape of its external protection or the nature of its internal processes, is modified by this incessant power of attraction and represents only the resultants of all the forces combined. Whether the first organisms were floating or sessile may have depended largely on the relationship of their own density to that of the surrounding medium. Theoretically, they may have resembled in shape and size the microscopic water particles of a cloud, composed of an aggregate of water molecules, developing with the help of an increasing surface tension, shape, additional energy and other matter, in a progressing entity. This theoretical concept of an organism may be too simple, but it shows the coordination of the forces we know. While the organism may have floated, carried along by currents of the surrounding medium, the development of undulating ability led slowly in higher forms of life to the most primitive self-propelling movements. Appendages for locomotion, such as the cilia of the Infusoria and Flagellata, the foot of the mollusks and the many legs of the arthropods, illustrate the great variety of walking mechanisms evolved by the invertebrates, although we know little about this evolution. The development of the locomotive mechanism in vertebrates has left more intelligible bits of evidence, which disclose the surprising ability of evolving organisms to adapt themselves freely to prevailing physical laws and to take advantage of the available irresistible flow of energy.

The basic structure of the mechanism controlling the locomotion of primitive vertebrates is the spinal column, which represents, with its numerous jointed members, a suitable flexible lever system, resembling that of a chain belt. It permits the fundamental movement of the most primitive form of locomotion, the gradual bending of the posterior portion of the body in a horizontal plane, and the consecutive gradual stretching of it, against the ground resistance of the curved portion, in the desired direction. This motion ultimately developed the multiple undulating movement of many fishes and the snakes. A more rigid body structure led to the evolution of the caudal fin, which remained largely a continuation and a function of the spinal column, permitting accelerated speed and direction control with less disturbance of the internal processes.

Later, some ancient acanthodians apparently developed lateral rows of scales, spike-like appendages, or horizontal ridges. Although fully exoskeletal, such structures may have led to the development of primitive fins and gradually to the pectoral, and finally to the pelvic, girdles. The exact functions of these fins are not very well established; but they may have been used for paddle-like locomotion, and particularly for moving on the bottom, a habit still possessed by some living fishes, such as the fresh water mud minnow, *Umbra pygmaea*, which leaves tracks of the paired fins on suitable medium covering the bottom. As all ground movements are exposed to a great amount of friction, which has to be neutralized by equivalent surface properties of the body, the function of the paired fins was probably primarily to elevate the animal above the ground, which required at least two successive, well-spaced, pairs of appendages. This resulted in the preserva-

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EXPLANATION OF PLATE 41

Chirotherium parvum (Hitchcock) Lull. Pes and manus cast. ×1. Milford, New Jersey. Upper Triassic. Brunswick formation. Holotype S490. (p. 410)

Bock, Triassic reptile tracks

Bock, Triassic reptile tracks

tion of energy and prevented external ground abrasion.

Progressive development of the fins, and lightening of the body by suitable internal organisms may have freed the fishes from dependence on the bottom and made the members of this group ultimately the masters of the waters. The previously employed bottom friction of the undulating type had been changed to a purely water friction, which expressed itself in the far speedier locomotion so well utilized by the *Selachii*. Although all the functions of the fins found on fossilized early fishes are not fully known, the paired ones of the living *Pisces* are retained chiefly as stabilizers, and for steering and braking. However, the caudal fin and the body, if sufficiently flexible, still represent the fundamental locomotive organs.

The physical conditions to which the fishes were exposed in the water were certainly not all disadvantageous and do not entirely explain the migration to dry ground, which may primarily involve a problem of distribution and ecology, rather than inadequate physical surrounding. The generally accepted picture of a descendant of the crossopterygians stepping out of clear water onto the good earth, certainly involved several intermediate environmental stages, in which the tetrapod-to-be must have lived close to the land, in a mud and swamp belt, where he may have acquired the first necessary respiratory modifications. Then he may have adventured onto mesophytic plants, thus probably developing a means of locomotion fairly well adapted to a terrestrial life. We can only assume the coordination of these phases, but a living tropical fish, *Periophthalmus barbarus* (Jordan and Seale, 1906) may suggest some of the stages of this evolution. This fish is able to climb the limbs of mangroves and raise itself up temporarily on its specialized pectoral and ventral fins, which are closely arranged behind the head. Whether such a fish would ever evolve into an amphibian we shall never know. There seems to have existed some biological resistance to the development of parallel lines of evolution in this direction, as the long history of the lungfishes testifies.

It is believed that the Devonian rhipidistian Crossopterygii (Gregory and Raven, 1941) were the ancestors of the tetrapods, although Holmgren (1939) has expressed the opinion that the first form must have been derived from shark-like predecessors. At any rate, Gregory and Raven (p. 340) seem to agree that the fishes having rhipidist paddles eventually came from shark-like ancestors. The phalange, including the carpals and metacarpals, are believed to have budded from a zone along the mesomeral border, which ultimately gave rise to the basal digit formula of primitive reptiles. That of the older amphibians is reduced and is approached, according to Williston (1925), by that of the later Cynodontia and some tortoises.

The fossil evidence also seems to indicate that primitive pectoral and pelvic girdles were basically established when the protetrapods advanced onto the land. But these animals were hardly in a position to assume an elevated posture with such a limb structure. It doubtless required a long period of evolution before the bottom dwelling fishes developed a hydrostatic mechanism sensitive enough to negotiate the gradually varying specific weight of the water column, whose pressure is double that of the atmosphere at a depth of 15 meters. Emerging from the water, the body weight of the fish increases considerably, on account of the different specific weight of the two media. As it can be assumed that the fins of the early sharks were flexible and not rigid, the mode of locomotion of the early tetrapod may be adequately pictured by comparing it with the clumsy movements of the living seal, *Phoca vitulina*, dragging itself laboriously about on dry ground because of the overwhelming force of gravitation.

Gradually biological efficiency and slow evolutionary repetition of the aquatic phases succeeded in eliminating the body-ground friction, although not completely,

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EXPLANATION OF PLATE 42

Chirotherium parvum (Hitchcock) Lull. Pes cast. ×1. Milford, New Jersey. Brunswick formation. Upper Triassic. Paratype. S488. (p. 410)

by elevating the dragging body with the help of greatly modified elements of the paired appendages. As the girdles of some fusiform fishes, which are believed to be the ancestral stock of the tetrapods, are rather narrowly built, the raising of the body would have required the development of an increased balancing ability and a widening of the girdle radius. As the fins were believed to have been pressed down originally by the body weight, the most important development was that of the knee action, which was achieved by the angled arrangement of the upper and lower leg portions, of which the latter became vertical, representing the elevating element, also to be used as a prop, while the former remained in its more primitive and original position, being nearly horizontal and largely functioning in this plane, extending the width of the area of body support. Thus the fin became partially an element of lateral extension and one of support. This system provided modest, but sufficient, elevation, saving an extensive lifting mechanism. The most active and initial locomotive function became invested in the foot, the position of which had to be horizontal and about parallel with the body axis. The movements of the main members forming the legs of the reptilians have remained largely three-dimensional until today. Some of the dinosaurs alone succeeded in reducing the angled position of the bones forming the knee, adapting a somewhat upright posture, which moved the knees around under the body and narrowed the width of the supports on the ground. This had to go hand in hand with a progressive balancing ability, due to the loss of support area; but it ultimately resulted, as many dinosaur tracks of the Triassic testify, in a purely bipedal, almost linear, two-dimensional method of locomotion, which has been only more recently acquired by a few mammals. That the bipedal mode of reptiles has not lost its usefulness is shown by the bimobile gait of the living *Basiliscus*, which prefers the upright posture when accelerated speed is essential. But the movements of this reptile's legs remain similar to those of the primitive reptilians, three-dimensional and swung in an outwardly curved motion, depressing the body in the opposite direction. The walking mechanism of the birds followed essentially those of some dinosaurs and was more or less duplicated, during the long evolution of the mammalian locomotor, by the primates.

While the structural mechanism is best illustrated by the dinosaurian reptiles, the principles of the locomotive device in earlier reptilians are basically the same. To appreciate the correlations between the kinetic actions of body movements and those of the constant physical vector forces, the results may be expressed best by the behavior of a simple static body. The movement of a pebble in a water flow, or from a mountain side, reflects not only the irresistible energy induced on the object, but also the destructive influence on its structure. The shape of the moving stone will permit it either to slide or to roll. Both methods will ultimately reduce it to its smallest constituents. But the difference between the two modes of movements will have this result, that the rolling pebble may have travelled ten times as far as a sliding pebble of similar size before its total disintegration. The variation of the ever important coefficient of friction in these two basic methods of locomotion is expressed in this relationship. This great abrasive effect, caused exclusively by gravitation, is always a difficult problem in biological maintenance of the locomotor.

This considerable difference in the amount of energy involved between the sliding and the rolling friction one would expect to see widely utilized in biological construction. But there exist barriers, which nature wisely avoids rather than stubbornly pursues. If a biological structure is formed to roll, its whole interior organism must rotate with it. This design has been tried in some primitive animals and is displayed by the radiating locomotion of some sea-urchins, which progress like a wheel having no rim, but numerous spokes. This method was never widely adapted because of its disadvantages, which were avoided by evolving a similar, equally efficient, construction. The locomotive principles of modern wheel movements around an axle, which is technically the most efficient method known, could not be adapted by a biological body, as the continuing rotary movement would have to be energized by attached muscle systems, which

could not achieve a full rotation without twisting or severing the muscles.

But similar partially revolving methods are employed in the mechanics of terrestrial locomotion by the specialized arrangement of the limb system. The first principle is the partial rotary movement of the limbs using the foot as a fulcrum. Although not continuous, it permits an effective rotation of the body close to 180°, which normally, for efficiency reasons, is far below this value, averaging about 60°.

The second mechanical principle, which acts physically in opposition to the first, is based on the pendulum, which only proceeds in one direction, but assures a minimum of resistance.

Hand in hand with these two mechanical applications works a static principle, requiring that the functional lever system must always form an unfailing support system to avoid wasteful body friction, and that the center of gravity must be largely confined within the support area.

The diagrammatic expression of the kinetic and static structure of the biological locomotor is shown in figure 1. The two basic movements of the legs form, (a) a sector (*A-B-C*) which comprises the rotary movement of the leg around the foot, (fulcrum *A*) when transporting the body one step (*B-C*), and (b) a trapezoid (*A-C-D-E*) in which the opposite leg provides the actual energy to lift and propel the body, the other completing a pendulum movement of two steps (*A-E*).

The rotary movement (*B-C*) is much more skilful and efficient, as might be expected. The action is technically a rotating lever system, energized by the opposite leg, which would have to elevate the whole body from the ground, should the maximum angle of 180° be required. However, a much smaller step angle, about 40° to 50°, is the average at slow pace, which reduces the uplift energy to the height of the segment. (*F-F'*). At the normal step angle mentioned the total vertical elevation of the body would be about 10 per cent of the leg length. This still considerable extent is reduced through suitable manipulations of the limb levers in the slow pace of men, but is fully exerted in the trot gait. Without indulging in physical details, the energy involved, which has to be based on the angular velocity, is determined in bipeds by the weight of the body and the sine of the step angle, which becomes zero at the center line. Therefore, the smaller the step angle, the less the energy expended by the elevating limb. The actual energy spent by the support limb is confined to small amounts of friction in the joints and the ground contact friction, generally con-

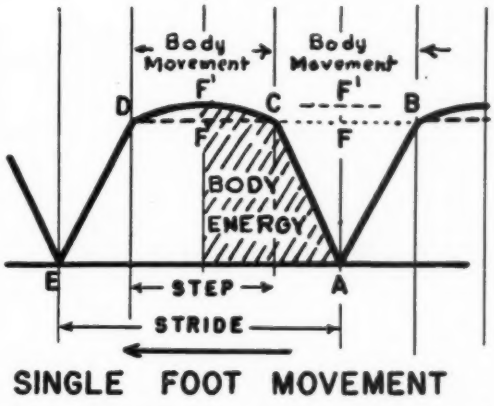


FIG. 1—Diagrammatic expression of kinetic and static relations in single foot movement.

centrated on the heel pad or metaphalangeal joint pads.

The first phase of the pendulum movement (*C-D*) starts with the greatest expenditure of energy, the elevating action, as explained in the preceding paragraph for the function of the opposite leg. This process is energized by the rolling-off motion of the foot leverage, requiring for the initial movement the greatest moment of force supplied by the longest lever, which gradually diminishes, as shown by the normal dimensions of the phalanges, with dwindling requirements of energy towards the zero point at the apex of the rotary movment (*F'*). The roll-off movement is not only the finest application of mechanics, it is also highly efficient, for it provides a peripheral rolling motion, instead of a sliding one, which greatly reduces the ground friction losses. When the apex at the middle line is reached, the entire leverage system of the limb is extended and the leg is charged with potential energy by its former action, swinging rapidly forward with a velocity about four

times that obtained by the propelled body. It arrives in time at its opposite pendulum position (*D-E*) to receive the potential energy of the declining body, regained from the primary uplift movement.

This represents the full ground function of a single leg (two steps), and its expenditure of energy is characterized by a nearly sinuous curve, whose wave length is one phase of locomotion (one step) and whose amplitude reflects the lifting power. This relatively small amount of physical energy additional to the small frictional forces is

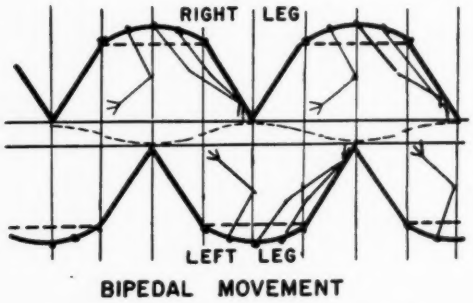


FIG. 2—Diagrammatic expression of bipedal movement.

the difference between the efficiency of wheel movements and the biological oscillating lever locomotion. However, there are many other practical advantages involved, which makes the latter propelling method still more desirable because of its more reliable terrestrial distributing powers. At a normal pace, the locomotive lifting energy amounts to only approximately 10 per cent of the body weight, which is not considerable and would only require a modest power mechanism. But as the latter is competent in man to move about three times the total body weight, it is clear that such an organism is equipped for peak loads, including the use of the most inefficient saltatorial movements.

The free pendulum action can be observed in figure 2, which shows that it actually starts in about the middle of the movement, as the preceding motion is used for propelling the body. The time element involved is controlled by the simple physical pendel formula of a full swing, which is $T = \sqrt{l/g}$, wherein l is the pending length of the leg.

The latter does not represent quite a mathematical pendulum, but rather a compound one, as its mass is distributed over its whole length. Furthermore, its fulcrum is not at rest, but proceeding half a step, and its length may vary with the physical requirements of the propelling velocity. Such a pendulum may become an enigma for a mathematical approach, but measurements prove that a full oscillation is completed within the pendulum velocity laws at a normal pace, when the foot is about to contact the ground. This clearly demonstrates that the body speed is synchronized with that of the leg pendulum. By that a great waste of energy is prevented, as the moment of inertia of the swinging leg is considerable on account of the high velocity and the weight of the limbs, which may reach 35% of the total body weight in men. If different velocities are required in the pursuit of biological sustenance, loss of some energy may be unavoidable. But many of the tetrapods develop a normal natural speed and stride, which synchronizes with the pendulum actions of their limbs, although the advantage may be negligible in the smaller kind on account of muscular friction.

As the pendulum speed is correlated with the size of the step, it is possible to determine the walking velocity of a tetrapod from its track pattern. Should a scale be established for the normal speed of the different tetrapods, it may permit us to conceive a more exact length of the limbs, which is now only possible by comparative deductions.

The pendulum principle may explain another synchronous motion, which otherwise appears quite problematical. We know that the pendulum movement of the leg in bipeds constitutes only an advancing oscillation and never returns, as it temporarily changes to a different physical element. When proceeding at normal speed, the forelimbs of some bipeds will oscillate freely in synchronization with the movements of the rear limbs, but their direction will be opposite. When the hind leg swings forward, figure 2 shows that the body also advances. The fore leg will not participate in that movement. However, the moment of inertia will produce an opposite force, which will start a pendulum movement in the reverse direction. This motion does not seem to save any particular energy; but it serves

as a counter action of the body inertia, imposed by gravitation, when the body descends from its highest position. This kinetic synchronism seems to explain also the adherence of the primitive tetrapods to the cross, or diagonal, walk (Kreuzgang), and there is no evidence that the quadruped reptilians have ever used any other symmetrical form of locomotion.

In figure 3, the quadruped gait can be observed, which also shows the adjustment between the stride of different sized legs, in which case the pendulum motion varies according to the difference of length. The center of gravitation of the body follows a nearly straight line for this type of locomotion. When, during further evolution, more narrow girdles restricted the ground area and shifted the feet closer to the middle line of the body, causing a lateral pending motion, additional balancing capacity was required before the second basic locomotion, the lateral walk, (Pass Gang) which is peculiar to some mammals, could be adapted. The lateral shift of the center of gravitation is shown in figures 2 and 3. The shaded area represents the time element, in which energy is expended. It must be admitted that it is not possible to show in the graph the distinction between the cross and the lateral walk. An additional dimension is necessary for demonstration, as the difference between the two types of locomotion is merely a differentiation of time elements. This actually permits an unlimited combination of locomotive methods, of which only those are practiced which agree with the kinetic expression of terrestrial energy reflected by fundamental physical laws.

Looking back at the primitive locomotion of the Crossopterygii, and following up the intricate path of locomotive evolution to that of man, we will have to admit freely that during this long period somebody has used quite a bit of mathematics.

DESCRIPTION OF THE TRACKS

Order SAURISCHIA

General classification.—The order of Saurischia is subdivided by Williston (1925) into the suborders Theropoda and Sauropoda, each comprising numerous families, the earliest of which has been found in the Keuper. In his "Short Review of the Lower Tetrapods" von Huene (1948) gives an excellent classification of the Saurischia, which he divides into two suborders, the "Coelurosauria" and the "Pachypodosauria." He lists 31 families, of which ten belong to the Coelurosauria. His fundamental distinction between the suborders is that the Coelurosauria had thin-walled bones, while the bones of the Pachypodosauria were strong and thick-walled.

The Triassic Saurischia of North America, which comprise five types, all from the Connecticut River area, were assigned by von

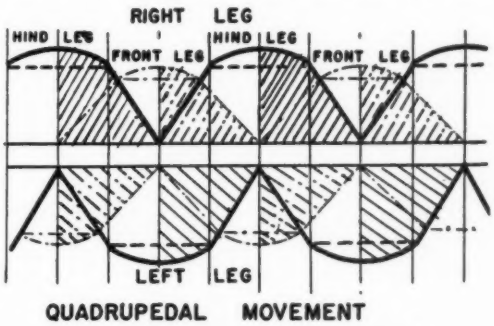


FIG. 3—Diagrammatic expression of quadrupedal movement.

Huene (1932) to the Coelurosauria with the exception of two forms, *Yaleosaurus* (*Anchisaurus*) *colorus* and *Thecodontosaurus* (*Anchisaurus*) *polyzelus*, which he placed in the family Thecodontosauridae, of the Pachypodosauria, although the two species have distinctly thin-walled bones. It is certainly difficult to make a convincing assignment from the material available.

While in other continents, particularly Europe, skeletal remains of the Saurischia are far more frequently found than is the evidence of their locomotion, the opposite conditions prevail in the Triassic beds of North America. It is therefore not surprising that saurischian tracks have received more attention in this country. The greatest sources of information are the basic contributions of C. H. and E. Hitchcock (1836 to 1889) and the revisional work of Lull (1904, 1915), in which the latter author lists eight families under the suborder of Theropoda, with numerous genera and species to account for the prolific dinosaurian tracks from the Triassic of the Connecticut Valley.

The evidence available from Europe is rather meager (Weiss 1934, von Huene, 1932, 1941) and the imprints reported by

these authors have not been so far closely correlated with osseous remains. The saurischian skeletons from the Connecticut Triassic have been correlated by Lull (1915) with specific tracks, which were doubtless made by some of these reptiles.

The more important theropodan foot imprints are grouped by Lull into several genera, two of which, *Anchisauripus* and *Gigandipus*, have a rotated hallux, and into the more slenderly shaped Grallators, including the large and bulky *Eubrontes*, the latter probably approaching the size of *Chirotherium rex*. The first two genera are mainly distinguished by the position of the hallux, while the remaining two are not known to impress the first digit. As the position of the toes may be largely functional, the recognition of these genera may not always appear to be justified; but there are an additional number of minor generic differences which add further weight to Lull's classification of the tracks.

Suborder COELUROSAURIA
Family GRALLATORIDAE
Genus GRALLATOR E. Hitchcock
GRALLATOR CUNEATUS E. Hitchcock 1858
Plate 45, figure 1

Grallator cuneatus E. HITCHCOCK 1858; —— R. S. LULL 1904, 1915.

Pes, digit no.	II	III	IV
Digit length, mm.	60	81	65
Phalang. pads			
length, mm.	25-19	21-25-20	16-14-11-9
width	15-16	16-15-13	12-11-9-8
thickness	7-6	8-6-4	5-4-4-3
Digit angle, degrees	28	25	

Total length, 98 mm. Total width, 61 mm. Length of step, 375 mm. Track surface, 21 cm.^{2} Track volume, 13 cm.^{3}

Digits.—Toes straight, three impressed, somewhat thicker at posterior end, well divided by digital pads, contracting margin at intersections. Middle finger longest, but advanced at base about one pad length and two pads protruding above tips of adjacent digits.

Pads.—Well developed, roundish, with pronounced intersectional crease, all distinctly impressed. No heel pads or other digits apparent.

Claws.—Long and broad, slightly smaller than adjacent pad, clearly offset from the latter. Shape ovate, acuminate, slightly curved. Sole horn indistinct, but some claws showing diminutive sole horn pads.

Record of functions.—Gait bipedal, tridactyl, digitigrade. Trackway angle about 155°. Rolling-off movement of phalangeal chain normally continuous, but last two pads of middle toe functioning solitarily. Lateral shift of pressure toward second digit.

Discussion.—This grallatorial track pattern is clearly distinguished from that of the similar genus, *Anchisauripus*, and related genera by the more diverging angle of the digits and a longer middle toe. It is only slightly smaller than *Grallator cuneatus* Hitchcock from Turners Falls, Massachusetts, but otherwise so nearly identical that it seems justifiable to include it in this species. It is also reported by Hitchcock from the Milford horizon 5.3 km. above the base, while our tracks were found at Schwenksville and Sanatoga, about 2.0 km below the Milford strata. Dinosaur tracks of this size were repeatedly reported from similar Brunswick horizons and there is no doubt that this type was a frequent visitor to the Triassic flats.

Lull (1915, p. 200) relates the smaller *Grallator cursorius* Hitchcock to the compsognathoid dinosaur, *Podokesaurus holyokensis* Talbot, and relates the similar sized *Grallator tenuis* Hitchcock to *Ammosaurus solus* Marsh, which would indicate that both animals were of corresponding dimensions, although they were morphologically quite different. Heilmann (1926) compared *Grallator tenuis* with *Procompsognathus triassicus* Fraas, from the German Stubensandstein, and fitted it quite successfully into the Connecticut track. As there is little difference between the imprints of *Grallator tenuis* and *Grallator cursorius*, it is baffling to think that three different families may be involved in these similar tracks. At least, it shows that footprints have to be very carefully scrutinized, before they can be useful for more exact correlations. The best that can be stated is that the small Grallators represent the small Coelurosauria, and that Heilmann's connecting link between *Grallator tenuis* and *Procompsognathus triassicus* identifies the Stubensandstein as a correlative horizon.

One important trackway from the German Triassic is called by Weiss (1934, pp.

5–11) *Dinosaurichnium schlauersbachense*. It was found in the Blasensandstein of Franconia, slightly below the Stubensandstein. It shows two consecutive footprints of an apparent Coelurosaurian, about half the size of those of *Grallator cuneatus* and almost identical with the trackway of *Grallator gracilis* C. H. Hitchcock from Milford, New Jersey, and Turners Falls, Massachusetts. It is one of the smallest dinosaurian tracks so far known, suggesting an animal the size of a small chicken. No corresponding osseous remains have been found. A single track, also resembling somewhat that of *Grallator gracilis*, is reported by von Huene (1941, p. 14) as *Coelurosaurischnus toscanus*, from the Italian Verrucano formation. From the upper Buntsandstein of Germany Kirchner (1927) has described several tracks as *Saurichnites auraensis*. These tracks appear to be those of chirotheriids, rather than saurischians. Little osteological information has been afforded by the *Grallator* tracks, and the size and position of their phalanges remains doubtful.

Lull (1915) believed that the phalangeal pads displayed by the Triassic reptilian tracks should cover the shanks rather than the joints. Soergel (1925, fig. 29) apparently followed Lull's suggestion. Peabody (1948) reconstructed the foot of *Grallator cursorius* in the opposite way, having the pads covering the joints, which theory he based on comparisons with the foot of the domestic turkey. Peabody must have overlooked the discussion of this subject by Heilmann (1926, p. 180), where the latter cited a number of birds, like *Corvus frugilegus*, the position of whose pads is different from those of the turkey. As pointed out before, the functional character of the foot largely determines its structure, and we may expect variations of pad positions on the toes of the same foot. One takes a chance in judging a phalangeal formula on such a rather uncertain basis, particularly in regard to Upper Triassic horizons, where similar Cynodontia tracks may be found. Heilmann's reconstruction of the foot of *Grallator tenuis* supports his comparison with the foot of *Procompsognathus*, although the reconstruction was made from incomplete material; but his illustration (fig. 130, k) hardly proves a general systematic trend of the relationship between the pads and phalanges.

Location.—These tracks were found by Earl L. Poole of the Reading Museum, Reading, Pennsylvania, in the Brunswick formation at the Squirrel Hill Quarry near Schwenkville, on Perkiomen Creek, Pennsylvania. The beds consist of reddish-brown, hematitic shale and intercalated sandstones. Horizon about 3,300 meters above the base and of Stubensandstein age.

Repository.—Poole Collection, Reading Museum, Reading, Pennsylvania. Holotype No. 15240.

Family GIGANDIOPODIDAE ?
(Anchisauridae) Lull
Genus GIGANDIPUS ? (ANCHISAURIPUS)
E. Hitchcock
GIGANDIPUS ? (ANCHISAURIPUS)
MILFORDENSIS Bock, n. sp.
Plate 43, figure 3

Description.—The tracks of this species are associated with the footprints of *Chirotherium parvum*, bearing the number S488 in the Hitchcock Collection at Lafayette College. There are two casts of left foot impressions of two different specimens, which almost touch each other. One is only partially preserved, while the other is complete and is considered herein as the holotype. The dinosaur tracks were already impressed when the *Chirotherium* crossed the same spot diagonally, touching the tip of the dinosaurian middle toe imprint and dislocating it slightly. Otherwise the cast is well preserved, revealing a good many details. The formula follows:

Pes. Digit number:	I	II	III	IV
Digit length, mm.	29	42	71	67
Phalang. pad				
length, mm.	10-9	21-11	21-19-18	19-16-12-10
width, mm.	7-6	18-15	18-19-17	11-10-9-9
thickness, mm.	1-1	8-6	4-5-6	3-5-7-6
Digit angle, degrees	73	18	15	

Total length, 94 mm. Total width, 65 mm. Track surface, 27 cm.^{2} Track volume 13.5 cm.^{3}

Digits.—II to IV closely arranged, slightly diverging, conical shaped, round at base, becoming gradually slender toward pointed claw. Lateral margin of digits contracted by shape of roundish pads. Middle toe thickest and longest, but position slightly advanced in relation to adjacent toes. Behind base of digit II there is a faint impression of a small, straight hallux at about right angles to the middle toe, indicating a position higher on the leg (7 mm.), just above the base of the second toe. Base of digits II to IV, broad, about 45 mm., indicating a relatively heavy dinosaur.

Pads.—Phalangeal pads well developed, thick, roundish, flexible, distinctly divided by creases and slightly at varying angles to each other, indicating functional position of phalanges or pads when impressing. Pad of hallux indistinct, flat. Heel pad of middle toe faintly visible.

Claws.—Digital terminals crowned by acuminate, broad, strongly built claws, distinctly offset to the adjacent pad, having a triangle-shaped base, all about of equal size, 10 to 12 mm. long, 8 mm. wide. Angle of base of claw to pad from 14° to 18°, suggesting flexible, strongly curved claws. Triangular base representing sole horn with two roundish, diminutive pads covering the posterior half of the sole horn with a central, wedge-like recess between the protrusions and a faint center line toward the tip of the claw.

Record of functions.—Though no consecutive footprints of this species were found, the gait is considered to have been bipedal, based on the generally recognized habit of the genus. Foot position digitigrade. In the first rolling-off position the hallux and first pad of digit IV, with the inconspicuous heel pad of digit III wedged between, make initial, though weak impressions, followed consecutively by the first pad of II, and the second pad of IV. In this position the pads are quite deeply impressed, indicating a heavy impact of the body. The next phase is shown by the impressions of the second pad (II digit) second pad (III digit) and third and fourth pads (IV digit), the depth registering an equally heavy impact. The continuing rolling off movement is carried alone by the broadening pads of the middle toe, while the lateral toes disconnect from the ground. The main pressure of the body was exerted on the inside portion of the foot. The small double pads of the sole horn suggest that they may have joined somewhat in the motion of the locomotive elements exposed to surface friction.

Discussion.—These tracks, doubtfully assigned to Hitchcock's genus *Gigandipus*, are rather modest in size compared with those of the single species of the genus shown by Lull (1915, p. 191), which is about five times as large. They are really closer in dimensions to *Anchisauripus hitchcocki* Lull, but they are distinguished from this genus by a more rotated hallux. The functions of this toe are apparently of a supporting nature, but, as this type of saurischian proceeded in a nearly linear, single line trackway, comparative studies show that the hallux may have interfered with ordinary walking functions, striking the leg, unless it is retracted to a more neutral backward position, characteristic of the genus *Anchisauripus*. Therefore, this awkward inclination of the hallux in our species may be a functional variation that might be expected, and the wisdom of considering it characteristic of a distinct family may be seriously challenged. However, differences in tracks are generally believed to reflect greater ones in the skeletal structure, and additional anatomical details leave no other choice than to include this species provisionally in Lull's Gigandipodidae.

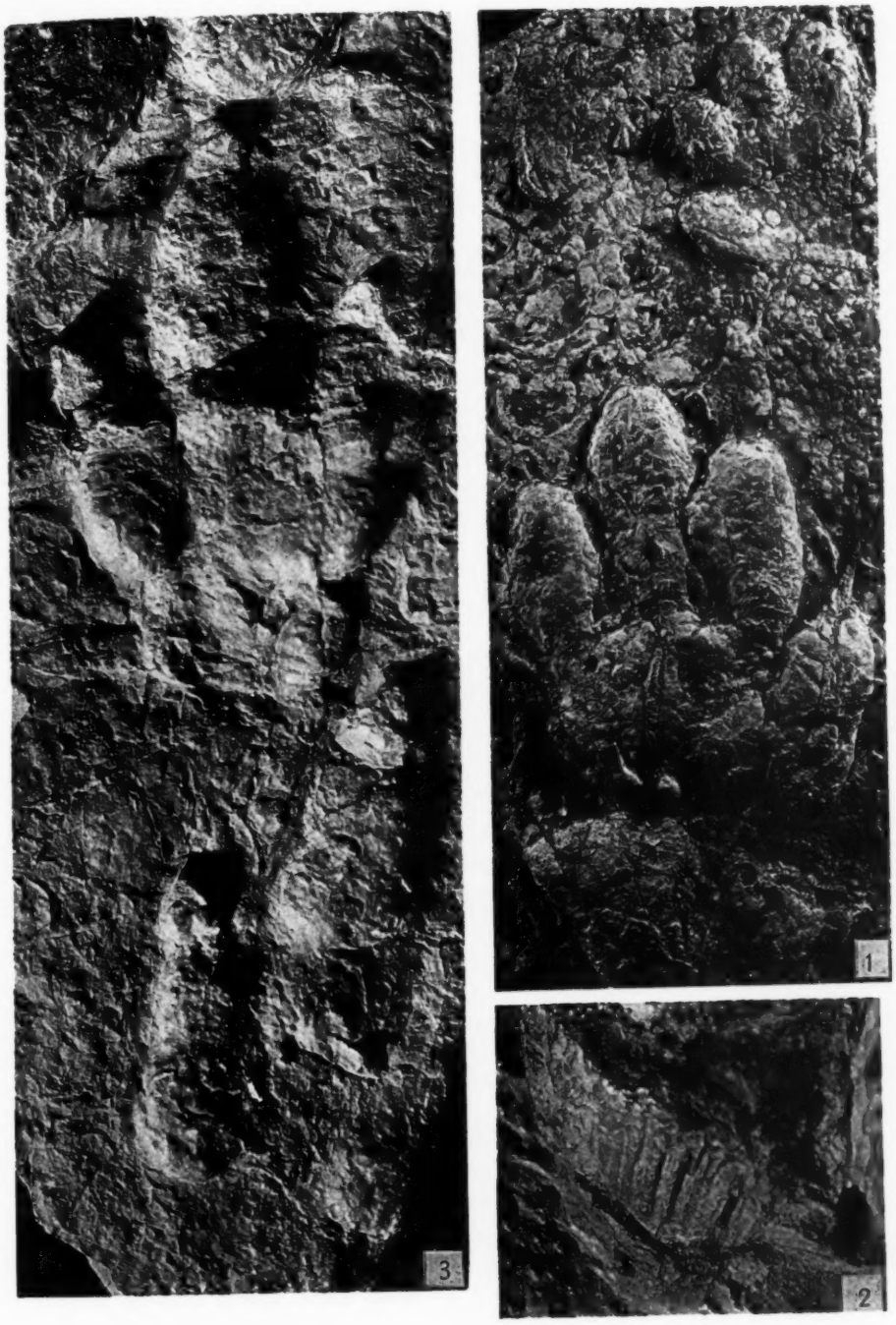
Lull (1915) compared the foot imprint of *Gigandipus* with those of the huge *Allo-*

EXPLANATION OF PLATE 43

FIG. *1*—*Chirotherium copei* Bock. Pes and manus cast. ×1. Milford, New Jersey. Brunswick formation. Upper Triassic. Holotype. No. S491. (p. 414)

2—*Chirotherium parvum* (Hitchcock) Lull. Cast showing grooved tip of toe. ×2. Milford, New Jersey. Brunswick formation. Upper Triassic. Paratype No. S488. (p. 410)

3—*Gigandipus ? (Anchisauripus) milfordensis* Bock. Casts of two left foot impressions. ×1. Milford, New Jersey. Brunswick formation. Upper Triassic. Holotype. No. 15210. (p. 403)



Bock, Triassic reptile tracks

Bock, Triassic reptile tracks

saurus from the Morrison, for an estimate of size. *Anchisauripus sillimani*, which is about one third larger than our specimen, is correlated by Lull (1915, p. 141) with *Yaleosaurus* (*Anchisaurus*) *colorus*, and it is believed that a similar type made these Milford dinosaurian tracks, although they have a pronounced predaceous character.

Unfortunately, there are no reports of similar imprints from Europe, but we may come to some conclusions by comparing *Yaleosaurus* with European skeletal remains. On account of some resemblance with the Thecodontosauridae von Huene (1932) included *Anchisaurus colorus* Marsh, as *Yaleosaurus colorus*, in this family, whose holotype was reported first from the English "Lettenkohle." There exist few similar characteristics and comparable elements with the exception of some minor bones and the teeth. The latter resemble those of *Iguanodon*, which have a peculiar serrated margin. Similar teeth have been found in the Lockatong, near Phoenixville, (*Thecodontosaurus gibbidensis* Cope). However, *Yaleosaurus colorus* does not have any serration. As this genus, furthermore, has pronounced thin-walled, hollow bones, the important criterion of the Coelurosauria, one may have doubts whether this genus should have been included in this suborder.

The Triassic Coelurosauria were generally swifter and smaller reptiles. However, the inclusion of the Upper Triassic family Halticosauridae, of which *Halticosaurus liliensterni* von Huene (1934) is about four times as large as *Yaleosaurus*, has since considerably widened its scope. If one compares the hand of the predaceous *Pachysaurus ajax* von Huene (1932, pl. 11) with that of the five times smaller *Yaleosaurus*, and if one compares the foot of this species with that of *Pachysaurus wetzelianus* von Huene (1932, pl. 12, fig. 10), one can hardly conceive that the tracks of these species could be told apart except by their size, although their osteological structure is different in many elements. The family *Halticosauridae* is chiefly known from the Stubensandstein, while the still larger built non-predaceous *Plateosauridae* are best known from the overlying Knollenmergel. Only a few species of the latter genus were found in the Rhaetic. There is no doubt that the large tracks of the Connecticut Valley and Whitehall, New Jersey, representing *Eubrontes giganteus* E. Hitchcock, may well match up with those of *Plateosaurus* or the similar sized *Pachysaurus*, which is abundant in the German Knollenmergel. Von Huene (1932, pl. 12, fig. 10) shows the left foot of *Pachysaurus wetzelianus*, whose size will fit well in the huge track of *Eubrontes giganteus* E. Hitchcock. Not only are the dimensions, such as length, thickness and position of the phalanges, close, but the presence of the well defined first toe rounds up a picture of close relationship to the likewise huge *Gigandipus caudatus* E. Hitchcock, from Turners Falls. While these large species have not yet been found at Milford (although known from the slightly lower horizon at Whitehall, New Jersey) four typical track patterns of the uppermost strata in the Connecticut Valley are present, including the large *Sauropus barrattii* E. Hitchcock, together with numerous plant fossils, which provide ample evidence that the Milford horizon compares well with the strata of the uppermost Stubensandstein, and particularly with the overlying Knollenmergel. Although some proof of overlap in the Rhaetic is evident, it appears to be insufficient to raise the horizon at Milford to a higher level. The tracks, plants and algal fossils of this locality also solved another problem of great importance. The beds of these strata dip considerably in a northwestern direction; and it has been repeatedly asserted (J. K. Roberts, 1928, D. B. McLaughlin and B. Willard, 1949) that these layers have been inclined originally by the nature of their deposition. It should be clearly stated that all track evidence shows that the imprints were made on a horizontal surface and that the thallus of the finger alga and plant stems in situ were all arranged vertical to the bedding plane. The fossil plant

EXPLANATION OF PLATE 44

Anchisauripus gwyneddensis Bock. Single pes imprint with single track of *Gwyneddichnium majore* Bock. ×1. Lockatong formation. Upper Triassic. Gwynedd, Pennsylvania. Holotype. No. 15222. (p. 406)

beds also show that they were laid down on a horizontal level.

Location.—Abandoned quarry of Smith Clark, Milford, New Jersey, 1.25 km. north of the Delaware River bridge. Upper Brunswick formation, 5,100 meters above the Triassic base. Correlative age: Knollenmergel.

Repositories.—Lafayette College, Easton, Pennsylvania, Hitchcock Collection. Holotype No. 8488.

Family ANCHISAURIPODIDAE
Genus ANCHISAURIPUS Lull
ANCHISAURIPUS GWYNEDDENSIS
Bock, n. sp.
Plate 44

Description.—This impression was found as a single rather shallow footprint on a large slab, which was covered with numerous tracks of different types of reptiles. It is a significant find, as it represents the only known dinosaurian evidence of reptilian locomotion from the Lockatong formation. The formula follows:

Pes. Digit number.	II	III	IV
Digit length, mm.	81	104	71
Phalang. pads,			
length, mm.	31-40	32-35-30	10-10-17-13
width, mm.	22-24	20-28-30	10-10-12-10
thickness, mm.	4-3	1-4-8	2-3-2-2(?)
Digit angle, degrees.	20	15	

Total length, 120 mm. Total width, 81 mm. Track surface, 33.5 cm.^{2} Track volume, 17.5 cm.^{3}

Digits.—Three visible toes, closely arranged, slightly diverging. Lateral digits curved to the outside, and margin contracted at intersections of pads. Middle toe longest and thickest, increasing in width toward the tip until running out in partially embraced claws. Base of digits broad, 72 mm. wide.

Pads.—Not all clearly defined, flat with rather straight margins and faint creases between pads. No heel pads or other digits visible.

Claws.—Shape ovate, accuminate, not offset from adjacent pad. Sole horn flat, showing no surface details.

Records of functions.—Gait considered bipedal, tridactyl, digitigrade. Rolling-off position of phalangeal chain normal. Lateral digits starting first, being joined in the second phase by the middle toe, which ends the roll-off function solely with the terminal pad. Angle of pads slight, but greatest functional pressure in the center of impression. Slight lateral shift of pressure to second digit.

Discussion.—This species closely resembles *Anchisauripus parallelus* E. Hitchcock, from the Turners Falls region, although the latter left a minute impression of the hallux, the outstanding mark of the genus. Our track does not reveal any evidence of the presence of the first toe, and it should be included properly in the genus *Eubrontes* (Lull, 1915, p. 195), in which Hitchcock grouped all larger tracks of this type showing no hallux. As pointed out previously, such a classification must remain artificial, as the impression may largely depend on the properties of the recording medium. However, relying on some lesser evidence as the claws, pads, and shape of the digits, we feel justified in including this track in the genus *Anchisauripus*.

There is one stratigraphically important difference which cannot be overlooked. The beds at Gwynedd, Pennsylvania, where our specimen was found, are about 1,300 meters above the base of the Triassic, while the similar Milford saurischian tracks are 3,800 meters higher in the section. The lower beds, which are known for their fish, phytosaurian, estheriid and plant remains, are the oldest strata known in this region, containing tracks of theropodians. This evidence corresponds well with that known from the European "Schilfsandstein-Bunte-Mergel series," the earlier portion of the middle Keuper, when the Thecodontosauridae made their first appearance. It is strengthened by the fact that one of the largest *Eubrontes* species (Lull, 1915, p. 196)—the *Anchisauripus* minus the hallux—left one of the oldest tracks of the Connecticut Tri-

assic, these tracks being found in the lower shales, which appear to be in age slightly younger than the strata of the Lockatong formation.

The only saurischian osseous remains from eastern Pennsylvania are two teeth described by Cope (1878) as those of a *Thecodontosaurus*, from the lower Lockatong margin, at Phoenixville, Pennsylvania, which compare in age with similar fossils from the Schilfsandstein. As this type is reported from the Lettenkohle, and the genus compares in general size with that of our tracks, we may assume that a type like *Thecodontosaurus* was one of the early representatives of the saurischians that roamed over the Lockatong mud flats.

However, we can hardly conceive that the Lockatong or the preceding Lettenkohle were the cradle of the saurischians; for that the known species were too well advanced in structure and size. Von Huene (1932, p. 93) has assigned a rather large tooth of *Teratosaurus(?) schützi* E. Fraas from the upper Muschelkalk to the Carnosauriers, and Jaekel (1910) reported a somewhat smaller tooth from the lower Muschelkalk, referred to *Zanclodon silesiacus*, which Williston (1925, p. 292) placed in the Anchisauridae, a family also used by Schmidt (1928, p. 432) for the genus *Thecodontosaurus*. One of the oldest evidences of saurischian appearance was recorded by Soergel (1925, p. 88), who reported dinosaurian footprints from the Buntsandstein; but he gave no further details or references. There is good reason to believe that the origin of the saurischians will be traced back to the earlier Triassic, but conclusive proof for the existence of dinosaurians below the Keuper still seems to be lacking. Nevertheless, this comparison affords a vivid picture of their extent through sections of the Newark basin, with its earliest appearance in the lower Lockatong formation.

Location.—Lockatong formation, Upper Triassic, Gwynedd Tunnel deposits, Gwynedd, Pennsylvania, 1.3 km. above base. Correlative age: Schilfsandstein-Bunte-Mergel series. Tracks impressed on the surface of bluish-gray argillite, weathering brown, representing the final phase of a flood deposit. Tracks of different, smaller, reptiles are abundantly represented, together with the remains of finger-shaped algae and small rain drop imprints. These beds are also known for their fishes, and for *Gwyneddosaurus* and *Gwyneddocarus*.

Repository.—Academy of Natural Sciences, Philadelphia. Bock Collection. Holotype No. 15222.

Family OTOUPHEPODIDAE
Genus OTOUPHEBUS Cushman
OTOUPHEBUS POOLEI Bock n. sp.
Plate 45, figure 2; plate 46, figure 4.

Description.—This single impression of a foot, in brownish shale, was obviously imprinted in the mud when the mud was still quite soft, obscuring somewhat the real shape of the pes. The details made out are as follows:

Pes. Digit number:	II	III	IV
Digit length, mm.	46	80	52
Phalang. pads,			
length, mm.	26-20(?)	30-24-26(?)	15-14-12-11(?)
width, mm.	16	30	21
thickness, mm.	5	9	8
Digit angle, degrees	13	18	

Total length, 85 mm. Total width, 61 mm. Track surface, 29 cm.^{2} Track volume, 15 cm.^{3}

Digits.—Three toes visible, of which the middle digit is the longest, and the second shorter than the fourth. Middle digit extraordinarily wide, with its posterior portions extending over the base line of the adjacent digits. Obscure striation between crotch of digits suggests a creased minor web.

Pads.—Base pad of middle toe particularly large, with finely granulated surface structure. Tubercles about 1.5 mm. wide. Remaining pads indistinct. No claws visible.

Record of functions.—Apparently bipedal, tridactyl, digitigrade. Rolling-off position normal, all pads acting jointly with adjacent ones except terminal pad of III, which func-

tioned alone. Lateral pressure strongest on IV.

Discussion.—In size and shape this species resembles *Otouphebus minor* Lull, from the Triassic of the Connecticut Valley, and it is only slightly smaller than the new *Gigandipus* (*Anchisauripus*) species from Milford (p. 406). Our species does not display any claws and also possessed a more pronounced middle digit, which distinguishes it from Lull's species. Some distortion may have been caused by the soft underlying medium. The single protrusion of the last terminal pad would also suggest relationship to the *Anchisaurus* group, although no hallux imprint is registered. The granulated surface pattern is believed to represent some dermal structure and resembles in size and pattern that of a chirotherid (see Peabody, 1948, pl. 40, fig. A). As the saurischian skin is mostly smooth, or rarely indistinctly wrinkled, one may wonder whether this track represents a chirotherid go-between.

Location.—The track was found by Earl L. Poole, of the Reading Museum, Reading, Pennsylvania, at the Squirrel Hill Quarry near Schwenkville, Pennsylvania, in the same beds in which the tracks of *Grallator cuneatus* Hitchcock (p. 402) were found.

Repository.—Academy of Natural Sciences. Philadelphia. Holotype No. 15223.

Order ORNITHISCHIA. (?)
Family Unknown
Genus PLATYPTERNA E. Hitchcock
PLATYPTERNA LOCKATONG Bock, n. sp.
Plate 47, figure 2

Description.—Only one single foot imprint of this problematic animal was found, of which the main dimensions follow:

Pes. Digit number.	II	III	IV
Digit length, mm.	125	162	132
Width (max.), mm.	42	30	27
Digit impress. mm.	14	11	10
Digit angle, degrees	20	18	

Total length, 252 mm. Total width, 148 mm. Track surface, 84.2 cm.^{2} Track volume 48.4 cm.^{3}

Digits.—Three toes, middle digit longest, II shorter than IV. All straight, conically shaped, spike-like, accuminate. No pad distinction. Faint, roundish heel impression. Claws not distinct nor offset. Functions apparently bipedal, tridactyl, digit-, or semi-digitigrade.

Discussion.—Although saurischian in proportions the shape of the digits appears fundamentally different. The absence of distinct pads or joint creases and the conical straight shape, suggest a foot not very well equipped for normal walking functions. The dimensions of the impression also indicate that the track was made by an animal light in weight, probably not more than 50 kg., which is considerably less than that of *Chirotherium parvum*, which weighed about 180 kg., although the digits of the latter species are shorter. From this one known track it is difficult to ascertain to which group of animals this new species belongs. Lull (1915, p. 226) included a large number of Hitchcock's genera in a rather voluminous incertae sedis section, to which he refers the genus *Platypterna*, which is seemingly closest to our track.

Location.—Gwynedd Tunnel deposits, Gwynedd, Pennsylvania, Lockatong formation, about 1.3 km. above the Triassic base. The track was found on a slab of hard grayish shale, and is from the same horizon as the new species *Anchisauripus gwyneddensis*.

Repository.—Academy of Natural Sciences, Philadelphia, Pa. Bock Collection. Holotype No. 15224.

Suborder PACHYPODOSAURIA
Family OTOZOIDAE (?) Lull
Genus OTOZOUM (?) E. Hitchcock
OTOZOUM (?) LINEATUS Bock, n. sp.
Plate 48, figure 1

Description.—A fairly well preserved pes and manus impression of this species is shown on slab S490 in the Lafayette College Hitchcock Collection, along with the type track of *Chirotherium parvum* Hitchcock. The dimensions follow:

Pes. Digit number	I	II	III	IV
Digit				
length, mm.	65	68	70	58
max. width, mm.	15	17	17	12(?)
Digit pads, mm.	30-20-15	24-22-22	22-20-19-19	25-15-18(?)

Pes. Digit number	I	II	III	IV
Total length, mm.	125			
Total width, mm.	75			
Manus. Digits,				
length, mm.	38	72	58	38
width, mm.	12	14	11	10(?)
Total length, mm.	80			
Total width, mm.(?)	68			

Pes with four digits, which are straight, parallel, rather slender, cylindrical, and well spaced. Pads distinct, rectangular, slightly rounded at corners, separated by a deep crease. Base of digits nearly straight. Terminals roundish, with indistinct, narrow, protruding acuminate claws. One broad, flat, indistinct heel pad. Functions, quadrupedal, pentadactyl, probably plantigrade.

Manus with four digits which are straight, parallel, and cylindrical, some being rather indistinct. Three to four pads to each digit, each about as wide as long, and several distinctly separated by narrow intermediate folds, or minute pads, characteristic of the manus, and apparently not used exclusively for locomotion.

Discussion.—Lull (1915, p. 225) described as *Otozoum minus* another track that is about twice as large as our species, but has not the pronounced straight, cylindrical digits. It is very interesting that the coordinated manus, which may have had only a limited use for locomotion, discloses double creases, or intermediate pads, which may indicate that the observable manus pads were not for protection of the joints, but were separated at the latter point, providing the space for curving the fingers inwards. Lull has pictured such minor folds in the genus *Anomoepus* E. Hitchcock, but they seem to appear mostly in the pes, where their usefulness can not be readily explained. He has grouped this family and several others with the Orthopoda (Ornithischia) without further comment.

Nopcsa (1923, p. 145) believed that the tracks of *Eubrontes*, *Platypterna*, *Otophebus*, and other genera resemble *Iguanodon* tracks, but are not identical. He places *Otozoum* Hitchcock in the Plateosauridae type, the species of which, however, was considerably larger and was mainly bipedal. It seems that this family is not very well suited for this comparison. A larger track, from the Upper Triassic of South Africa, showing a similar kind of straight digit, is referred to *Euskelosaurus africanus* Haughton (1924) by von Huene (1932, p. 213), who compared it with the genus *Plateosauravus*.

A single pes track, similar to ours and from the same locality, is shown on plate 46, figure 1. It may belong to this species, but it is somewhat larger and makes quite a chirotherid impression, an observation which Nopcsa (1923) also made when comparing the genus *Otozoum*. However close the relationship may be, the characteristic fifth finger of *Chirotherium* is missing, just as the large claws of the manus, outstanding in the Plateosauridae, are absent in our species.

Location.—Abandoned quarry of Smith Clark, Milford, New Jersey, at the same horizon at which *Chirotherium parvum* and *Gigandipus milfordensis* were found.

Repository.——Hitchcock Collection. Lafayette College, Easton, Pennsylvania. Holotype No. S490.

Order THECODONTIA
Subordei PSEUDOSUCHIA

General Classification.—Williston (1925) arranged the two suborders Pseudosuchia and Phytosauria, out of a total of four, in the order Parasuchia. Von Huene (1948) divided the order Thecodontia into the suborders Pseudosuchia and Parasuchia, the latter including the Phytosauria. The suborder Pseudosuchia of von Huene (1948, pp. 76–87) comprises all remaining thecodontian forms, of which the most important are, in regard to our discussion of Triassic reptile tracks, the group Chirotherioidea, to which Abel's (1935) track family Chirotheriidae should be added, and the family group of small pseudosuchians. Von Huene also believes that the Chirotherioidea are the precursors of the Ornithischia and the Euparkeriidae those of the Saurischia.

Family CHIROTHERIIDAE Abel, 1935
Genus CHIROTHERIUM Kaup, 1835
CHIROTHERIUM PARVUM (Hitchcock) Lull
Plates 41, 42

Otozoum parvum HITCHOCK (1889)
Chirotherium parvum LULL (1915)

Description.—Two separate slabs of shale show the cast of a correlated manus and pes impression. The first slab, which bears the number S490, Hitchcock collection of Lafayette College, Easton, Pennsylvania, apparently was the type which Hitchcock used for his description and is herein also treated as the type specimen. The second slab, bearing the number S488, on which the fifth toe section of the cast is broken off, is treated as the paratype. It comes from the same horizon at Milford, New Jersey as does the holotype. This is indicated by the attached original label, written by Hitchcock. Both type impressions represent identical species, but they can hardly have been made by the same individual, to judge from some varying details. For convenience in comparison the general dimensions and digit formula of the type and paratype are grouped together.

Position of digits and pads.—Pes digits closely arranged, somewhat club-shaped, having rounded tips. Middle toe longest, slightly expanded in the anterior portion and somewhat overlapping the laterally adjacent digits. Tip of I toe nearly in line with base of middle toe. Tip of V digit not higher than base of metaphalangeal pads. V digit diminutive, retarded, little different from metaphalangeal pad. Metatarsal region showing distinct pads, passing gradually out toward tarsal region. Below the pad of III and IV digits, the V metatarsal pad forms a nearly triangular elevation, 20 mm. high, sloping down toward the tarsals.

Digit terminals.—Most conspicuous is the apparent absence of claws or toe nails, well developed in other species of *Chirotherium*. Tips of digits at ventral portions well rounded up to a depth of about 5 mm. If the foot is more deeply impressed, as is the case in the type specimen S490 (pl. 41), the toe terminals display a hoof-like, crescent shaped, parallel ridged reenforcement, protruding at an angle of 45°, disclosing no sign of an extended claw, although the toes seem to have been fully immersed in the

Type specimen No. S490

	Right manus					*Right pes*				
Digit number	I	II	III	IV	V	I	II	III	IV	V
Length (free), mm.	—	22	32	27	—	46	63	82	66	33
Width (max.), mm.	—	20	22	20	—	35	40	37	35	37
Digit impress., mm.	—	7	8	5	—	18	20	18	15	11
Metaphalang. impress., mm.	—	—	—	—	—	16	15	15	13	9
Digit angle, degrees		30	32				12	13	16	
Total length, mm.			72					185		
Total width, mm.			55					110		
Track surface, cm.^{2}			36					102		
Track volume, cm.^{3}			21					160		
Distance, manus-pes, mm.					185					

Paratype No. S488

	Left manus					*Left pes*				
Digit number	I	II	III	IV	V	I	II	III	IV	V
Length (free), mm.	—	—	—	23	18	40	62	71	62(?)	—
Width (max.), mm.	15	22	16	13	13	26	32	37	32	—
Digit impress., mm.	22	27	28	20	12	11	11	10	4	—
Metaphal. impress., mm.	20	26	24	24	20	6	6	4	3	—
Digit angle, degrees		—	—	—	—		14	16	14	—
Total length, mm.			72					—		
Total width, mm.			62					115		
Track surface, cm.^{2}			36					98		
Track volume, cm.^{3}			98(?)					78		
Distance, manus-pes, mm.					125					

ground (about 22 mm.). The ridges are 1 to 1.5 mm. apart and remain parallel to the long axis of the digit at the same angle and also along the small portion reaching around to the lateral margin (Pl. 42). The ridges are roundish and often substriated, reminding one of the structure of a fluted phytosaur tooth. The toe tips of the paratype are not deeply enough immersed to show the striated reenforcement pad, but on some the base can be observed.

Manus about one third of pes surface. Digits I to IV ovate, short, evenly sized, radiating. Tips well rounded without striated reinforcement pads or claws. V finger small, abortive but distinguishable. Phalangeal pads appear to be undivided. Metacarpal pads present but indistinct.

Discussion.—Literature on footprints, particularly those of chirotheriids, has become more extensive, with a great quantity of details drawn from the mostly meager evidence. It has helped to give us a vivid picture of this still evasive animal. Soergel (1925) has greatly advanced our knowledge in his paleobiological work about the *Chirotherium* tracks, which also have been treated skillfully by Watson (1914), Lull (1915), Kirchner (1927), Rueger (1929),Ruecklin (1936), Kuhn (1936), von Huene (1936, 1941), Lilienstern (1939), and Peabody (1948). Many problematical questions have been more or less satisfactorily solved, so that it would serve no good purpose to duplicate the available information here. However, some specific anatomical details and some stratigraphical and ecological considerations should be added.

Volume of imprints and weight.—The manus and pes of the type and paratype are differently impressed. In the type specimen the pes is strongly inserted in the mud and the manus only lightly, while the paratype imprints are just oppositely arranged. As the sum of the displacement volume is nearly constant, it is believed that the weight pressure of the paratype imprint was for some unknown reason concentrated on the manus. From comparisons with a dinosaur imprint on the paratype matrix and experimental impressions under different mud conditions, a method of determining the total weight of the animal was conceived. It suggests a weight of 180 kg. for this *Chirotherium* species with a possible error of 10%, which is close to the size of an adult brown bear.

General comparisons.—To judge from the character of the imprints and available comparative dimensions, *Chirotherium parvum* had a pes about one half the size of that of *Chirotherium rex* (Peabody, 1948), or two-thirds the size of *Chirotherium barthi*, both species from Lower Triassic deposits. Our species is otherwise distinct in its shorter and differently placed digits having well rounded tips, and in the apparent absence of claws. A footprint, pictured as that of a species of *Chirotherium* (Kuhn, 1936, pl. 13), from the Blasensandstein of the German middle Keuper, discloses relatively similar, though somewhat larger, features. The fifth toe is already reduced and more axially arranged. This seems to be significant, as the age of the tracks of these types is only slightly different.

Comparison of the digits.—An important development is the broadening of the toes in their upper half, the nearly equal length of the second and fourth digit, and the considerably longer third one. The digits have a roundish, plump shape, which does not suggest any phalangeal pattern, and they represent a considerable change from the more primitive types such as the small *Chirotherium diabloensis* (Peabody, 1948, pl. 34), which has long slender digits, with the fourth the longest. During the progressive development period, the fifth finger underwent considerable reduction, finally reaching an abortive stage, the form exhibited by *Chirotherium parvum.*

Digital terminals.—The pronounced claws, generally occupying the tips of the digits, are apparently absent in this species. If claws were present, they must have occupied the upper surface of the toe. The crescent-shaped frontal reenforcement pads (pl. 43, fig. 3), with well-developed ridges, indicate that they were equipped to withstand considerable abrasion forces. Such striated, hoof-like, pads have been observed on other specimens before, but were generally believed to have been caused by scale-like protrusions, when pressed deeply into the mud. This apparently is not the case here. These pads are slightly laid in, like finger nails, and they are evenly inclined at

an angle of 45°. At such an angle, the original pattern would not be deformed by sliding. The scales of the epidermis must also have been much smaller to have cut such definitely formed ridges. This may permit the conclusion that these terminal pads were an original anatomical development of this species to facilitate walking and reduce ground abrasion.

Comparison of the claws.—Soergel (1925) shows the lower side of a claw of *Chirotherium barthi* (fig. 18) with a central ridge, which he calls the sole horn. It is the horny, somewhat recessed, ventral side of the claw partially enveloping the terminal phalanx. In larger claw structures the sole horn may become a strong horny plate. If we compare the claws of different types of chirotheriids, it is noticed that the more primitive species of Buntsandstein age are equipped with long, sharp claws, often well curved, which Soergel (1925) believed to indicate carnivorous habits, though it should be stated that well developed claws are not uncommon with animals of non-aggressive habits. Peabody (1948, fig. 34) pictures *Chirotherium rex*, from the upper Moenkopi, with more blunt and shorter claws, which indicate a gradual reduction and broadening in shape from those of older types. The form of toe tips of *Chirotherium parvum* suggests that a still greater flattening out of the claw occurred, which finally may have been projected on the terminal of the digit having the function of a protective horny plate. It also may suggest that the functions of the digits became largely locomotive, reducing a pronounced aggressive aspect greatly. A similar development may have taken place with the toes of some elephants, whose claws are reduced to roundish plates. There is certainly no indication that the chirotheriids of the Upper Triassic developed a speedier locomotion, but from the shape of the foot impressions we may assume that their habits became largely slow-paced cursorial. As the dorsal portions of the digits cannot be judged, there still remains the alternate theory that the horny terminal pads were of mere dermal development, and the claws may have been in a retracted or elevated position, which may be suggested by two small disconnected terminal imprints (pl. 41).

The phalangeal pads.—The ventral pads of the digits and metaphalanges are considerably developed, being capable of extensive abrasive duty. From the groove, or crease, a thickness of 15 mm. of some of these cushions was measured, which would place the phalangeal bones rather high and close to the upper surface.

The phalangeal pads, proper, are not as clearly defined as in other species, particularly *Chirotherium barthi*, which is figured by Soergel (1925, fig. 28). The number of pads shown is believed by Soergel to represent an equal arrangement of the phalanges, which could not be the case in our species, as they apparently have only two digital pads. A reduced number is also observed in a similar species from Storeton, England, assigned to the Keuper (Cunningham and Sutherland, 1840, pl. 1). Soergel's interpretation was challenged by Peabody (1948, fig. 38), who based the position of the pads in relationship to the phalanges on the arrangement he found in the foot of a domestic turkey (fig. 37). It is true that some pads of the turkey are arranged over the joints, but it is just as well known that in numerous

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EXPLANATION OF PLATE 45

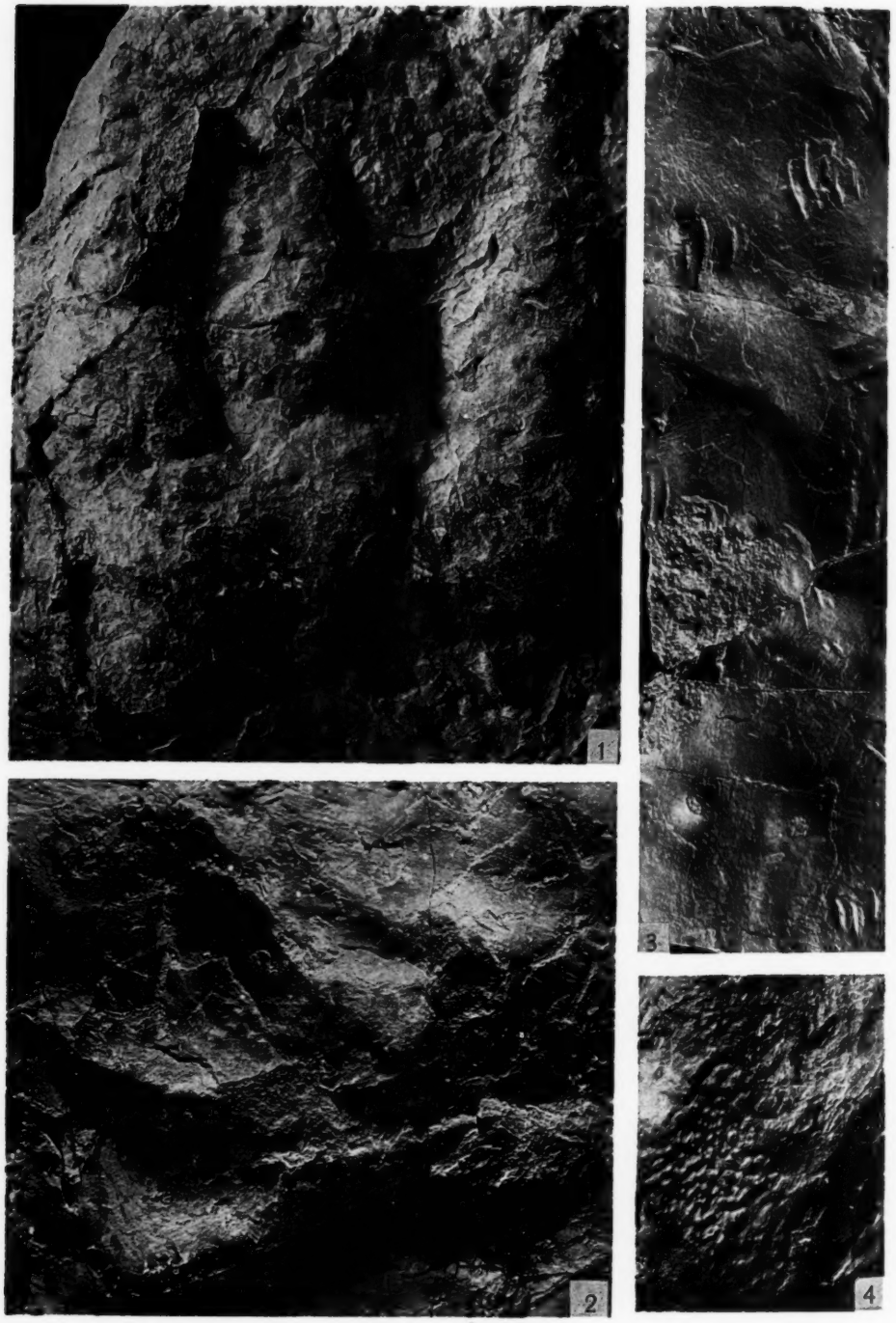
FIG. *1*—*Grallator cuneatus*, E. Hitchcock. Track pattern of one step and a single pes imprint. ×15. Schwenkville, Pennsylvania. Brunswick formation. Upper Triassic. Holotype. No. 15240. (p. 402)

2—*Otouphebus poolei* Bock. Schwenkville, Pennsylvania. Brunswick formation. Upper Triassic. ×2. Holotype. No. 15223. (p. 407)

3—*Kintneria brunswicki* Ryan and Willard. Track pattern of lacertoid or primitive saurischian. Gwynedd, Pennsylvania. Lockatong formation. Upper Triassic. ×1. Paratype. No. 15220. (p. 422)

4—Minute tracks (probably related to the *Kintneria* type) and imprints of a fine water spray. Gwynedd, Pennsylvania. Lockatong formation. Upper Triassic. Holotype. ×1 (not described). (p. 423)

Bock, Triassic reptile tracks



Bock, Triassic reptile tracks

other birds, such as *Pica pica*, the pads contact each other at the joints.

The problem involved is not only a morphological, but chiefly a functional one, which requires one to go into some detail concerning the relations between pads, phalanges, joints and muscles. It has been pointed out before that the lever system of the locomotive appendages may be compared with the links of a chain belt, which theoretically may complete an angle of just short of 360°. However, the functional angle of the extremities is much smaller, rarely exceeding 90°, although the locomotive maximum is close to 180°. The links of the human hand, which cannot be usefully adapted for walking, may be able only to bend inwards for grasping, and similar movements, while the phalanges of the foot must be able to incline in the opposite direction for proper walking positions. Many Aves, such as the domestic fowl, proceeding in a nearly linear track pattern, require the upward movement for the rolling-off motion and the opposite position for curving their toes in a closed, or fist-like, form to clear the adjacent leg when walking. It is also used for roosting, scratching, and as a protection against cold weather. While running, some of the birds do not have sufficient time to curve their toes, which remain stretched, and their body movements become undulating, producing a track pattern with a considerable track angle. The ostrich has overcome some of this difficulty by shedding the unwieldy toe altogether, being contented with two, which are provided with flat, broad pads. However, some of the birds which rarely come to the ground, having abandoned all cursorial habits, do not need their toes for roll-off movements and have their pads shifted from the joints to the shanks which position facilitates the downward motion of the toes. In purely arboreal types, such as *Patagona gigas* (pl. 50, fig. 2), the pads are subdivided, becoming lamellar, as in some living arboreal lizards.

The motions of the phalanges are activated by groups of small and larger muscles, including tendons, of which the extensor muscles operate in the upper portion and the flexors in the ventral section. It is the lower part of the foot, which is exposed to ground abrasion and shock, which requires additional protection. However, the greatest protection is required by the joints, as they are exposed to the greatest pressure, forming the fulcrum for the lifting power leverage during the roll-off movement. Fundamentally, they should be free to be functional; but the padding is of such a nature that it will permit the necessary tension without injuring the pad tissues. These considerations indicate that biological mechanics require free joints, while biological sustenance may modify these requirements with the varying functions of the structure, and we would arrive at the following conclusions:

1. For exclusive cursorial habits, the pads of the foot and hand should protect the joints.
2. For arboreal habits the pads of the foot should be divided at the joints.
3. The joints of the hands should be as free as those of the feet in purely arboreal types, but may become protected or lamellar, if used cursorially also.

As anatomical evolution may not always be able to keep step with the speed of habit changes, the functional requirements may not always agree with the anatomical facts; but the foregoing points may serve as a basis for closer conclusions, although reliable determinations can hardly be made from tracks alone without the proof of correlating osseous remains.

Peabody (1948, p. 401) further believes

EXPLANATION OF PLATE 46

FIG. *1*—Single pachypodosaurian track of chirotheriid character. ×1. Milford, New Jersey. Brunswick formation. Upper Triassic. Type No. 15230 (not described). (p. 409)

2—Pes imprint probably of a large parasuchian of the *Clespsisaurus* type. ×1. Gwynedd, Pennsylvania. Upper Triassic. Lockatong formation. No. 15231 (not described).

3—*Procolophonipus vonhuenei* Bock. Track pattern of a small Cotylosaurian. ×1. Phoenixville, Pennsylvania. Lockatong formation. Upper Triassic. Holotype. No. 15218. (p. 419)

"that the reptilian character of the phalangeal formula as established by Soergel is valid though derived by him mainly from a generalized assumption and that the unpadded feet of small chirotheriids afford a more positive indication of the phalangeal formula." In the absence of skeletal material, and in view of the functional nature of the pads, his finding cannot be taken entirely for granted. Neither could his finding about the unpadded digits of his smaller species be accepted, because doubts may be justified that they belong to the same genus. Examining his photographs, one cannot be too sure that the digits of the smaller types are distinguished rather by joints than by pads. Furthermore, the track of *Chirotherium lulli* (pl. 49, fig. 7) which is still smaller than that of *Chirotherium diabloensis*, shows distinctive pads similar to those of the larger species from Milford. The pads do not confirm so far with certainty the primitive digit formula of the reptilians. To distinguish joints one may have to turn to considerably smaller tracks, such as those of *Gwyneddichnium majore* (pl. 49, fig. 1), in which species the shanks can be definitely recognized.

Evolutionary remarks.—A comparison of the structural and anatomical features disclosed by the large Milford chirotheriids with those of the older Moenkopi (Peabody, 1948) and of the Buntsandstein from Germany, shows a distinct evolutionary trend toward a final, or rather fatal, form. The pes of the Upper Triassic types from the highest strata of the Brunswick formation is broadened in width and diminished in length. The digits are shorter, broader, closer set, and fleshier, having rounded terminals and apparently reduced claws, if any. Fewer pads, laterally compressed against each other, form a compact support surface. The reduced number of thick dermal pads indicate that the flexibility of the digits has been diminished, which weakened the proper roll-off movement, excluding speedy locomotion. This development may have been partially compensated for by the more axial transfer of the fifth digit under the foot, with the phalangeal part much reduced, and by utilization of its metatarsal element as an extensive support lengthwise, rather than laterally representing, with an enlarged, compound roll-off leverage, an intermediate phase of gait, which technically remains digitigrade. Moreover, the Milford chirotheriids never adopted bipedalism, as their tracks were always found with a distinct manus imprint, likewise of non-aggressive design. The general impression of the track maker, compared with similar types of the Moenkopi, is the emasculated appearance, which did not seem to match up greatly with that of the aggressive saurischian crossing its way (pl. 43, fig. 3). These reptiles represent the youngest of this type, as none have been so far discovered in higher strata, and they probably can be considered the last of the *Chirotherium* type that are known. Nevertheless, the different members of the *Chirotherium* family showed a remarkable record of sustaining themselves throughout the Triassic period, probably amounting to not less than 25 million years. The oldest reliable member is reported by W. Pabst (1908) from the German Permian, which would extend the origin of the chirotheriids still further back.

Location.—Abandoned quarry of Smith Clark, Milford, New Jersey, 1.25 km. north of the Delaware River bridge. Deposits consist of gray-blue Lockatong-like argillites and grayish sandstones, with occasional conglomerate layers, overlain by typical reddish-brown Brunswick shales and sandstones.

Age.—The *Chirotherium* foot imprints are associated with dinosaurian tracks (*Grallator* and others), finger-shaped algae (*Dasycladaceae*), imprints of raindrops, and small wood fragments. At the same horizon plant beds contain the foliage of an advanced form of *Ginkgo*, *Clathopteris* fern leaves and conifers, including *Cheirolepis*. These beds of the upper Brunswick formation, which are about 5,100 meters above the base, are believed to be beds represented by the Knollenmergel of central Europe.

Repository.—Lafayette College, Easton, Pennsylvania. Hitchcock Collection. Holotype No. S490. Paratype No. S488.

CHIROTHERIUM COPEI Bock, n. sp.
Plate 43, figure 1

Description.—The footprints of this species are represented by the cast of a single pes and a correlated manus in front

of it. Both are fairly well preserved and permit a dependable reading of the digit formula.

	Right manus					*Right pes*				
Digit number	I	II	III	IV	V	I	II	III	IV	V
Length (free), mm.	15	31	32	35	24	38	56	67	50	30
Width (max.), mm.	12	18	18	18	16	25	33	30	27	26
Digit imprint, mm.	3	5	6	6	4	9	10	8	4	12
Metaphal. impr., mm.	3	4	5	5	4	10	9	9	8	10
Digit angle, degrees	—	6	14	18		11	10	8	—	
Total length, mm.			67					180		
Total width, mm.			45					101		
Track surface, cm.^{2}			25					85		
Track volume, cm.^{3}			15					81		
Distance, manus-pes, mm.					155					

Digits and pads.—Pes digits I–IV closely arranged, broad, club-shaped, having semi-rounded tips. Middle toe longest, slightly expanding over tips of adjacent ones. V digit not distinguishable from metaphalangeal pad. I digit displaying one pad, II–IV digits two pads. Broad metaphalangeal pad below first four digits, being separated by deep groove (11 mm.) from V metaphalangeal pad. No claws disclosed.

Manus impression slightly larger than one-third of pes surface. Digits short, roundish, radiating. First digit diminutive. Only one digital pad noticeable. Metaphalangeal pads indistinct. Tips well rounded, without claws.

Discussion.—Chirotherium copei is distinguished from *C. parvum* by its smaller size and, in particular, by its more slender shape. The tips of the pes are not deeply enough impressed to show clearly the reenforcement pads at the terminal of the digits, though some traces are observable. The displacement volume of the pes and manus is about half of that disclosed by *C. parvum*. The body weight is estimated at about 96 kg., indicating a more moderate size. From these comparisons the large species from the Moenkopi formation, such as *C. rex*, may have had a weight of about 400 kg.

Location.—The slab was reported to have been found at a quarry near Washington's Crossing on the Delaware River. However, close comparisons with the rock and other fossils found on the matrix of the imprints of *Chirotherium parvum*, makes it reasonably certain that this species also came from the Milford, New Jersey, locality. Therefore, the same age correlations should be applied as is given for that species (p. 415).

Repository.—Academy of Natural Sciences, Philadelphia, Pennsylvania. Bock Collection. Holotype No. 15210.

CHIROTHERIUM LULLI Bock, n. sp.
Plate 49, figure 7

Description.—The well preserved imprint of a single pes, an indistinct, correlated manus in front of it, and the traces of an apparent manus behind the pes, comprise the record of this small *Chirotherium*, of which the track formula follows:

	Right manus					*Right pes*				
Digit number	I	II	III	IV	V	I	II	III	IV	V
Length (free), mm.	9	7	—	—	6	9	12	19	17	6
Width (max.), mm.	—	2	—	—	—	4	4	5	4	4
Digit imprint, mm.	—	1	—	—	—	1.5	2	1.7	1.3	1
Metaphal. impr., mm.	—	1.3	—	—	—	1.2	2	—	—	1
Digit angle, degrees	—	—	—	—		3	—	—	—	
Total length, mm.			14?					42		
Total width, mm.			12?					23		
Track surface, cm.^{2}			0.95?					2.94		
Track volume, cm.^{3}			0.2?					0.71		
Difference, man.-pes, mm.						46?				
Difference, man.-manus, mm.						92?				

Pes with digits I to IV clearly separated, with about 2 mm. space between. Shape straight and fairly slender. Tips roundish without distinct claws or terminal pads. III digit longest. Tip of first as low as base of III digit. V digit slender, indistinct, with heavy impressing metaphalangeal pad like those of digits I–IV, but separated from the latter by a space as wide as the pads. The digital pads are distinctly divided and follow a pad formula 2-3-4-5-?.

Manus impression quite indistinct, except for that of one straight, slender digit. Second manus merely vague imprint. Weight of animal about 2 kg., corresponding to that of a rabbit.

Discussion.—*Chirotherium lulli* is almost a replica of *C. copei*, but has more slender digits, and different pads, and is considerably smaller. The length of the pes is 42 mm., compared with 53 mm. for *C. diabloensis* Peabody (1948, p. 348), from which it is readily distinguished. Hitchcock (1858) established the genera *Chirotheroides* and *Batrachopus*, in which the pes is thought to have only four digits. Otherwise, they appear to have been quite *Chirotherium*-like in character. They were doubtfully included in the suborder Aetosauria, although the extremities of the latter are known to have had five digits.

Locality.—From the Brunswick formation of the Smith Clark Quarry, Milford, New Jersey, about 15 meters above the bed where *Chirotherium parvum* was found. The rock is hematitic red-brown, finely laminated shale, about 5,100 meters above the base of the formation. Only finger-shaped algae were found in this rock, which also contains small water flow marks.

Repository.—Hitchcock Collection, Lafayette College, Easton, Pennsylvania. Holotype No. S491.

CHIROTHERIUM(?) HUBERI Bock, n. sp.
Plate 47, figure 1

Description.—This is the largest footprint found in this region. Though the slab contains only the imprint of the pes, other tracks of the same type, including the manus, were present but could not be recovered.

Pes with digits I–IV distinctly separated, with about 20 mm. minimum space between them. Shape pointed, straight, conic, broadest in the middle section. Sharply pointed tips suggesting slender claws, 30 mm. long, with a vague sole horn impression. Middle digit largest, but only slightly so. Digital pads, flat, undivided. Metaphalangeal pads not impressed except V toe pad, located below IV digit.

Manus roundish in appearance. Digits cone-shaped, pointed, radiating. Pads undivided. Metaphalangeal pads not impressed.

Approximate weight 285 kg.

Discussion.—It is unfortunate that no better material could be secured of these significant impressions, of which a number were preserved in hard gray argillite. The size of the animal must have been close to that of *Chirotherium rex;* it is, however, clearly distinguished from the latter by its peculiar shaped, slender digits, and it is different from *C. parvum*, which has not pointed claws. The horizon seems to be similar to that of the *Chirotherium* species of the English Keuper from Storeton, though the species appear not to be any closer. There is also some resemblance to von Huene's genus *Thecodontichnus* (1941, pl. 2, fig. 2), but it is in other ways distinct. Our species may not have all the characters of the genus *Chirotherium;* however, it is provisionally retained in the latter.

Locality.—The imprints were found in

	Left manus					*Left pes*				
Digit number	I	II	III	IV	V	I	II	III	IV	V
Length (free), mm.	—	60	—	—	—	?	152	155	146	30
Width (max.), mm.	—	16	—	—	—	30	45	48	51	65
Digit imprint, mm.	—	1.5	—	—	—	1.5	2	2	1.5	—
Metaphal. impr., mm.	—	—	—	—	—	—	—	—	—	1.8
Digit angle, degrees						23		21		
Total length, mm.			80(?)					285		
Total width, mm.			70(?)					178(?)		
Track surface, cm.^{2}			64(?)					207(?)		
Track volume, cm.^{3}			34(?)					314(?)		
Distance manus-pes, mm.					355					

grayish hard argillite in Huber's Quarry, Belfry, Pennsylvania, in the lower Lockatong, about 1.1 km. above the base, suggesting an age equivalent to that of the German Schilfsandstein-Bunte Mergel group. In the same horizon in Huber's Quarry were found a jaw of *Clepsisaurus* Lea, a conifer, and finger-shaped algae.

Repository.—Academy of Natural Sciences, Philadelphia. Bock Collection. Holotype No. 15211.

Family group SMALL PSEUDOSUCHIAN
von Huene 1948
Family GWYNEDDICHNIDAE Bock, n. fam.

Description.—Small quadrupedal, pentadactyl form with digitigrade gait. Pes imprint larger than manus. Digits slender, well spaced, radiating. Third digit longest. Claws small. Phalangeal formula close to 2-3-4-4-3. Shape Chirotheriid-like, but more slender.

Genus GWYNEDDICHNIUM Bock, n. gen.

General character, that of the family. One genus only.

Genotype: *Gwyneddichnium majore*, Bock, n. sp.

GWYNEDDICHNIUM MAJORE Bock, n. sp.
Plates 49 and 50, figure 1

Description.—This not infrequently found track shows four pes and two manus imprints on a small slab, and other ones with identical tracks and a dinosaur foot impression, *Anchisauripus gwyneddensis*, which is the only dinosaurian track known from the Lockatong formation.

Pes-Manus digit number	I	II	III	IV	V	I	II	III	IV	V
Length, mm. Digits. #1	15	16	21	20	15	—	—	—	—	—
#2	18	?	20	20	15	—	—	—	—	—
#3	13	19	21	17	?	7	8	9	7	?
#4	12	15	20	20	12	6	7	10	9	5
#5	12	16	19	16	12	6	7	10	8	6
#6	?	15	18	18	10	—	—	—	—	—
Total width, max., mm.	20–22							14–15		
Total length, max., mm.	22–25							12–13		
Distance, manus-pes, mm.	15–18									
Distance, pes-pes, mm.	58–62									
Track surface, cm.²	0.78							0.38(?)		

Digits.—(Pes) Mostly five impressed, being straight, linear, about 0.6 mm. wide, apparently separated by joints or small pads, 1–1.2 mm. thick, some dot-like, others elongated. Shank thin, showing no padding. All digits mostly equally impressed, about 0.6–0.8 mm. wide. Three middle digits longer than lateral ones. Third digit longest, but sometimes equal to length of fourth. Phalangeal separation not distinct, but formula may be close to 2-3-4-4-3 or 2-3-4-3-3. Phalanges adjacent to metatarsals average about one half of total digit length. Metatarsals not impressed, but posterior joint impression occasionally shown, disclosing a length about that of the adjoining first phalanges. Compound digital base forming a moderate arch, which is less curved in the manus. Phalanges of latter not clearly distinguishable, but arranged like those of the pes. Claws small, inconspicuous, about 1–1.2 mm. long. Manus impression slightly behind pes imprint, somewhat shifted toward the inside.

Record of functions.—Gait considered quadrupedal, digitigrade, pentadactyl. No heel pad impressions. Pes and manus axially arranged, the former somewhat overstepping the latter. Initial rolling-off load carried about three quarters by all digits, while the remainder only involves the three middle toes, finally completed by insignificant solitary action of the third one. Step about length of three pes impressions.

Discussion.—The tracks do not resemble any previously described ones, and they display some unusual characteristics. The relationship of the manus and pes and the arrangement of the digits, with the third one the longest, suggests pseudosuchian affinities, but the thin linear digits, resembling their bony structure without showing distinct padding, removes the species from the Chirotheria. The digital picture excludes quite certainly the lacertoids, including the Protorosauria. Pseudosuchians

somewhat smaller than *Aetosaurus*, *Stegomus*, or *Typothorax*, may fit somewhat the pattern. However, *Typothorax meadei* Sawin (1947), is pictured with manus and pes digits, of which the third one may be the largest; but they appear to be considerably thicker and shorter, jointed with relatively long, heavy metatarsal elements. Recent crocodilian tracks show a certain similarity, having the third digit longest and a pronounced hypophalangy; but their first appearance is considerably later. Sawin (1947, p. 220), points out that the poorly preserved elements of the manus of *Typothorax meadei* show no similarity to those of the crocodile, as is the case with the pes. Therefore, tracks of the latter may easily mislead.

The proverbial scarcity of skeletal reptile remains literally forces us to a comparison with *Gwyneddosaurus erici* Bock, the small tetrapod from the same Gwynedd horizon, which has been previously considered to be of saurischian stock; but it is stated by von Huene (1949) that it is rather a protosaurian. Although no complete pes or manus assembly was preserved in *Gwyneddosaurus*, the arrangement of these bones suggests that the pes was about 2.5 times larger than the manus and the relationship of the digits similar. The latter of the fore limb range in length from 6 to 10 mm., and those of the hind foot from 18 to 25 mm. These dimensions would be well suited to leave a track similar to that of *Gwyneddichnium*. The peculiarly formed shoulder girdle, vertebrae, and other distinct bones of *Gwyneddosaurus* probably exclude it from any relationship with the Saurischia, in which it was included with reservation, but the same structures do not seem to bring it any closer to the Protosauridia, which are known from the Permian to the Middle Triassic. *Gwyneddosaurus* and the related tracks may well represent a new group, probably close to the small pseudosuchians, whose tracks are quite common in the Lockatong sediments. Other bones of the same species and related tracks were recently found at the same horizon.

Location.—Gwynedd tunnel deposits, Gwynedd, Pennsylvania. Lockatong formation. Upper Triassic. 1.3 km. above the Triassic base. This horizon is correlated with the European Schilfsandstein-Bunte Mergel series of the middle Keuper. The holotype is on a small slab of gray-blue, hard shale, weathering brownish, and the paratype is impressed on a large slab of similar material together with the new dinosaur track, *Anchisauripus gwyneddensis*.

Repository.—Academy of Natural Sciences, Philadelphia. Bock Collection. Holotype No. 15212, paratype No. 15213.

GWYNEDDICHNIUM ELONGATUM
Bock, n. sp.
Plate 49, figure 5

Description.—Only one single complete pes imprint of this species has been found, but faint impressions of the claws of the manus and other pes traces permit an analysis of the track pattern. The formula follows:

Pes. Digit number	I		II		III		IV		V
Digit length, mm.	5		9		13		8		6
Number of intersection	2		3		4		3		2
Digit angle, degrees		13		8		8		12	
Total width, mm.	8								
Total length, mm.	15								
Total surface, cm.^{2}	0.26								
Step, mm.	48								
Trackway width, mm.	12								

Digits.—Five, evenly impressed, being straight, quite slender, about 0.4 mm. wide at the shank portion, 0.8 mm. thick at the joints. The latter appear to be protected by pads. Three middle digits longer than lateral ones, third digit longest, protruding length of one phalange. Fifth digit placed far below remaining ones. Due to position of latter, compound base of all phalanges sharply curved, nearly resembling reversed number six. Phalangeal formula reduced, but not certain. Digital impression of manus only preserved in claw marks, and apparently in size not much smaller than pes.

Claws.—Small but sharp, about 1.2 mm. long, 0.6 wide, arrow-head shaped, some disclosing faint sole horn.

Functional record.—Gait apparently quadrupedal, pentadactyl, digitigrade. No heel pad or metatarsal pad impressions. Rolling-off load carried by all digits in the initial one third of the phase, by the three middle digits in the second third, and alone by the third digit in about the last third of the movement. Trackway pattern relatively narrow, resembling that of chirotheriids, indicating a narrow-built elongate, slender body, supported by medium-sized legs, with a tail that did not normally drag on the ground.

Discussion.—This track pattern shows a more pronounced pseudosuchian character than that of the genotype. It is also considerably smaller, about half the size. The tracks of both species are evidently closely related. Skeletal information may, of course, prove that they are generically distinct; but until such proof is found, this species should remain in the genus *Gwyneddichnium.*

Location.—Gwynedd tunnel deposits, Gwynedd, Pennsylvania. Lockatong formation. Upper Triassic, the same horizon as that of *Gwyneddichnium majore.*

Repository.—Academy of Natural Sciences, Philadelphia. Bock Collection. Holotype No. 15214; paratype No. 15215.

GWYNEDDICHNIUM MINORE Bock, n. sp.
Plate 49, figures 2–4

Description.—Several single tracks of this small reptile much resemble those of the preceding one, having the following dimensional formula:

Pes. Digit number	I	II	III	IV	V
Digit length, mm.	3	6	7	5	4
Number of intersections	2	3	4	4	2
Digit angle, degrees	15	12	12	14	
Total width, mm.	5				
Total length, mm.	11				
Total surface, cm.²	0.15				

Digits.—Total of five, evenly impressed, shape slender, with pronounced thickening of the joints, which may be pads, about 0.6 mm. wide. Three middle digits longer than lateral ones, second longer than fourth, third longest. Fifth digit placed below fourth digit, showing metaphalangeal pad.

Claws.—Small and pointed, about 0.7 mm. long, 0.3 mm. wide, slightly curved.

Functional record.—Gait apparently quadrupedal, pentadactyl, digitigrade. Terminal one-third of middle digit performing final roll-off movement.

Discussion.—Although no complete track pattern of this species is available, the similarity to the previously described one leaves no doubt that they are closely related. The observer may be tempted to group them in the same species, but the length and position of the digits separates them quite distinctly. The shape of the imprint resembles more that of a human hand than is the case with any others previously known except those of *Chirotherium lulli.* The pads in this species are quite close, showing no shank, so that it is impossible to come to any conclusion in regard to the correct number of phalanges. The pad formula is given as 2-3-4-4-2, which is close to that of the other two species. The fifth toe is very *Chirotherium*-like in its position and shape, but is distinguished from that of *Chirotherium lulli* by its size and more slender proportions. It may still be slightly smaller than that of the Recent *Basiliscus basiliscus.*

Location.—Gwynedd tunnel deposits, Gwynedd, Pennsylvania. Lockatong formation, Upper Triassic. 1.3 km. above the Triassic base. The horizon is the same as that of the remaining *Gwyneddichnium* species.

Repository.—Academy of Natural Sciences, Philadelphia. Bock Collection. Holotype No. 15216; paratype No. 15217.

Order COTYLOSAURIA
Genus PROCOLOPHONIPUS von Lilienstern
PROCOLOPHONIPUS VONHUENEI Bock, n. sp.
Plate 46, figure 3

Description.—The trackway pattern of a small reptile, consisting of several pes im-

prints, has the following dimensional formula:

Digit number	II	III	IV	V
Digit length, mm.				
Right pes	8	9	9	6
Left pes	7	9	8	5
Total width, mm.		10		
Total length, mm.		10–11		
Track surface		0.22(?)		

Digits.—Four toes visible, linear in shape, thin, pointed, well spaced, parallel, difference of length small, bases forming straight line. Upper portion slightly curved in outward direction. No pads or joints distinguishable.

Functional record.—Gait tetradactyl and apparently jumping quadrupedal, without leaving distinct traces of manus imprint. Rolling-off load, when walking, would be carried for the most part by all digits, indicating a slow moving, rather plump, reptile.

Discussion.—This track pattern is limited, by its peculiar arrangement of the digits, to two large groups, the Cotylosauria or the Chelonia. The latter produce imprints similar to those of our species, having digits more or less parallel and the connections with the metatarsals forming a nearly straight line, but they also show a distinct sole pad. The latter is not shown by our species, and the narrow track pattern also seems to exclude this order.

Cotylosaurian foot tracks have been described previously by Rühle von Lilienstern (1939, p. 7) as those of a new genus, *Procolophonicus*, from the German Buntsandstein. These imprints have some resemblance to those of our species. Although there may be some generic distinctions between the two, our tracks are referred to Lilienstern's genus. The presence of Procolophonidae in the Newark basin has been established beyond doubt by C. W. Gilmore (1928), who described the small *Hypsognathus fenneri*, further corroborated by the discovery of another specimen of the same species, described by Colbert (1946). Both reptiles were found in the Brunswick formation between Passaic and the first Watchung Mountain, New Jersey. The size of *Hypsognathus fenneri* is about twice that of ours, as indicated by the tracks. Unfortunately, complete osseous remains of the extremities are lacking. The picture of the fossil before preparation (Colbert, 1946, pl. 31, fig. 1) shows portions of a manus displaying about four distinct closely set metacarpals, with little divarication, and with its proximal ends forming a nearly straight line. For some reason or other the original position was changed in the attempted reconstruction (fig. 17) to a loosely arranged, quite arched, form. This deviation is also reflected in the life form restoration shown on plate 33, picturing a clumsy little reptile with almost identical sized manus and pes, having quite sprawling digits. Making some concessions to the intuition of the artist, and considering the original position of the fossilized metacarpals, one may conceive that a reptile of the *Hyposgnathus* type could have left a track similar to that of *Procolophonipus*.

In regard to the stratigraphic position of the latter, some comparison with that of the New Jersey species may be useful. The Pennsylvania tracks were found above Phoenixville, in the Lockatong formation, about 700 meters above the Triassic base. These strata are correlated with the "Schilfsandstein-Bunte Mergel" group of the lower part of the Middle Keuper. Investigation of the structural picture, based on the profile theory of vertex monoclines, indicates a level of 2,100 meters for the bed, where the specimen of *Hyposgnathus fenneri* from Clifton, New Jersey, was found, and an horizon, which is an additional 400 meters higher for the second specimen of that species. Such a position is slightly above the top of the Lockatong formation, which ranges in thickness from 600 to 2,000 meters in Pennsylvania. The upper portions of the Lockatong beds level out in the equivalent

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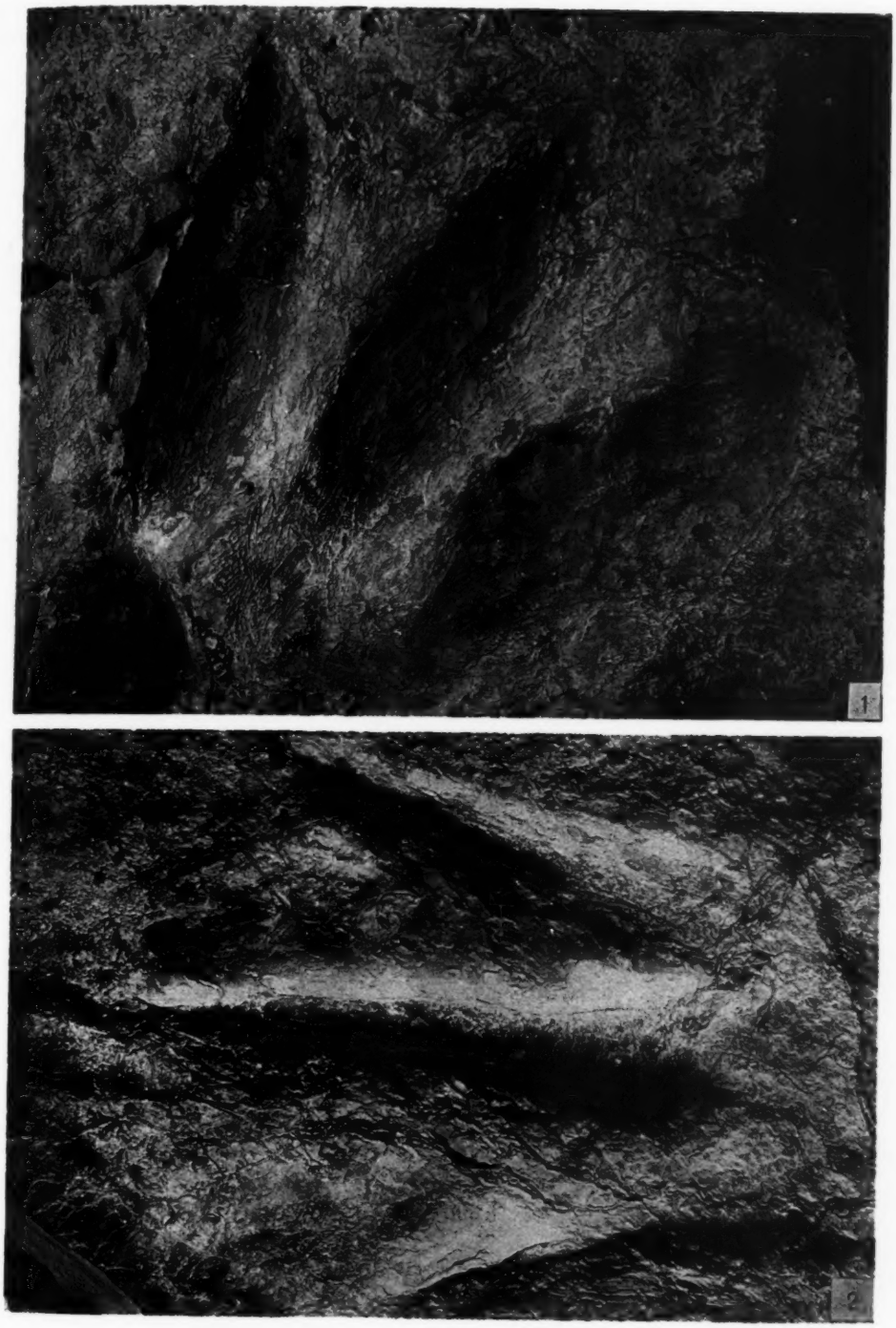
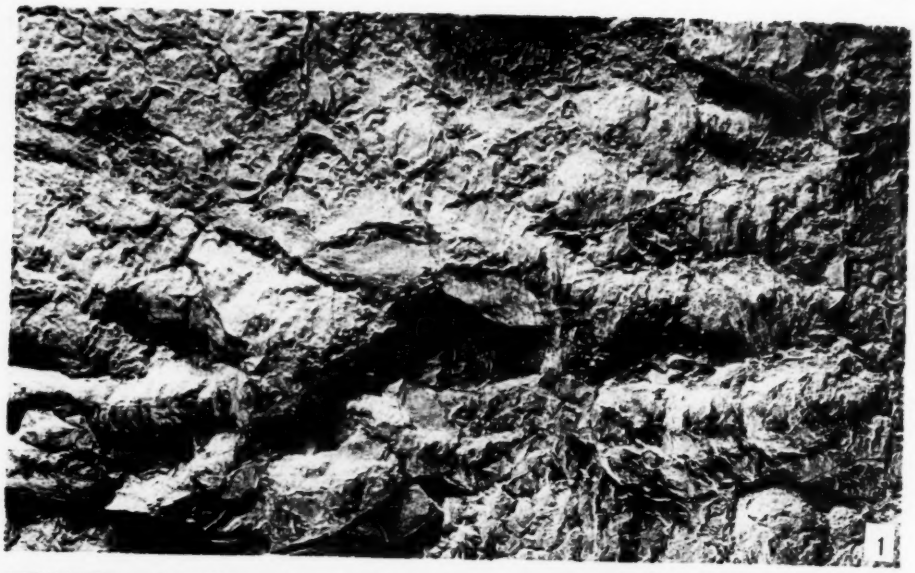
EXPLANATION OF PLATE 47

FIG. 1—*Chirotherium huberi* Bock. Pes imprint of large chirotherid with pointed toes. ×½. Belfry, Pennsylvania. Lockatong formation. Upper Triassic. Holotype. No. 15211. (p. 416)

2—*Platypterna lockatong* Bock. Single pes imprint, possibly of ornithischian origin. ×½. Gwynedd, Pennsylvania. Lockatong formation. Upper Triassic. Holotype. No. 15224. (p. 408)



Bock, Triassic reptile tracks



Bock, Triassic reptile tracks

of the Stubensandstein, and both *Hypsognathus* horizons may be correlated with it, as the extent of the Stubensandstein age reaches above the 3,000 meters level, where the first *Grallator* tracks in this section were found.

Location.—Drainage basin quarry, near Phoenixville, Pennsylvania, Schuylkill River, Lockatong formation, Upper Triassic. 700 meters above the Triassic base. The footprints are on a small slab of gray, hard, well-laminated shale.

Repository.—Academy of Natural Sciences, Philadelphia. Bock Collection. Holotype No. 15218.

Lacertoid reptiles

ORTHODACTYLUS E. Hitchcock

ORTHODACTYLUS HOWELLI Bock, n. sp.

Plate 48, figure 3

Description.—Several casts of the manus and pes representing this reptile are scattered over two small slabs, one of which also contains the cast of the foot imprint of *Otouphebus poolei* (plate 45, figure 2).

Digit number. Pes-manus	I	II	III	IV	V	II	III	IV
Length, mm. #1	24	34	37	30	—	8	11	13
#2	16	?	40	35	—	6	10	8
Width, mm. #1	2.5	3	3	2	—	1.5	2	1
Step, mm.	85–90							
Distance, pes-manus	10–15							

Digits.—Manus digits five, but mostly only three middle fingers impressing. Shape linear, thin, elongated, almost parallel to each other. Third digit quite long. Shank showing no padding, but phalangeal contacts slightly enlarged. Terminals pointed, but no distinct indication of claws. Pes cast showing only portions of first three digits in typical lacertoid, staggered, arrangement, placed slightly behind manus and at an angle to the latter.

Record of functions.—Gait quadrupedal, probably pentadactyl, digitigrade. Long fingers suggest similar sized toes, indicating an agile reptile of slender proportions. Axial angulation between manus and pes (about 25° to 30°) suggests jumping ability, similar to that of the Ranidae.

Discussion.—E. Hitchcock (1858) established the genus *Orthodactylus* for tracks corresponding to ours, though the manus and pes seem to be arranged vice versa. The divarication of the presumable manus is different from that of our species, but may have been caused by a variation of the gait. Schmidtgen (1927, p. 104, fig. 3) pictures three tracks of similar proportions from the German "Rotliegenden" near Mainz, leaving little doubt that these otherwise undescribed footprints should be referred to Hitchcock's genus.

One of the distinctions which seems to separate the pseudosuchians and dinosaurian tracks from the lacertoid reptiles, is the peculiar staggered, nearly parallel, position of the first three or four digits of the latter, particularly of the pes. In many species this is mainly caused by the outward-ly directed mesaxial position of the hind foot and by the pressure exerted during locomotion. Another important reason seems to be the greatly differentiated length of the digits and metatarsals, the latter being nearly parallel and closely set, particularly, in smaller types. The track pattern of some of the Protosauria is quite similar, and it is difficult to tell the footprints of both orders apart.

A typical lacertoid track pattern is excellently shown by Schmidtgen (1927, p. 103, fig. 2) as *Ichnium gampsodactylum staigeri*,

EXPLANATION OF PLATE 48

FIG. *1*—*Otozoum (?) lineatus* Bock. Pes and manus cast of a saurischian of doubtful relationship. ×½. Milford, New Jersey. Upper Triassic. Brunswick formation. Holotype. No. S490. (p. 408)

2—Pseudosuchian tracks from Phoenixville, Pennsylvania. ×2. Upper Triassic. Lockatong formation. Holotype. No. 15232 (not described).

3—*Orthodactylus howelli* Bock. Single track of pes and manus. ×1. Schwenkville, Pennsylvania. Upper Triassic. Brunswick formation. Holotype. No. 15219. (p. 421)

a representative of a German Permian genus established by Pabst (1908), which shows a rotated fifth digit, recalling superficially that of *Anchisaurus* Hitchcock, from which, of course, it differs fundamentally in the number, length, and arrangement of the toes, and in locomotion. The tracks shown by Schmidtgen seem to be identical with a new track genus, *Rotodactylus*, from the Moenkopi of Utah, of which Peabody (1948) described three new species. *Rotodactylus bradyi* (Pl. 30, fig. B, 2) is particularly not distinguishable from *Ichnium gampsodactylum*, which genus is, therefore, entitled to priority. There are some variations between these two genera of tracks which do not appear to be specific, and can hardly be generic. Differences of the position of manus and pes, including variations in the ratio of stride and size (*Rotodactylus mckeei* 6:1, *R. cursorius* 8:1, *Ichnium gampsodactylum* 4.5:1) are so related to changes in locomotor velocity and the character of the recording medium that they have to be evaluated with caution.

Peabody also refers his genus *Rotodactylus* to the pseudosuchians, essentially on account of the rotated fifth digit, without which, he claims, "the trackway might well have been called lacertoid" (p. 335). However, there seem to be no pseudosuchians known that have a fifth digit directed oppositely to the remaining ones; but this is a pronounced feature in some recent lacertoids. It is well known that the arboreal chameleons have some backwardly directed digits. The foot of the gecko, *Gymnodactylus miliusii*, would imprint a track probably little different from that of *Ichnium gampsodactylum*. Snyder (1949, pl. 1) pictures *Basiliscus basiliscus* in a bipedal running position, which exhibits a rotated digit. Furthermore, some of the geckos, and also *Anolis carolinensis*, display on the plantar surface of the foot transversely elongated scales or lamellae, bordered by granulated protuberances very similar to those described and pictured by Peabody in his species *Rotodactylus mckeei* (p. 335). In fact, some of the terminals of the digits show thickened portions resembling the scaly pads of the recent *Gymnodactylus pulchellus*. These comparisons seem to suggest that the genus *Ichnium* (Peabody's *Rotodactylus*), would be more at home among the lacertoids than among the pseudosuchians. Von Huene (1950, p. 57), who does not mention Schmidtgen's species, draws attention to the *Rotodactylus* tracks of Peabody in his paper about the origin of the Ornithischia. He believes that the imprints were made by an "extreme chirotherid" equipped with limbs for climbing. This functional diagnosis would not be particularly contrary to the above stated evidence that "*Rotodactylus*" may be rather a lacertoid reptile.

Location.—The tracks were found by Earle L. Poole, of the Reading Museum, Reading, Pennsylvania, at the Squirrel Hill Quarry, near Schwenkville, Pennsylvania, on Perkiomen Creek, in red-brown hematitic shale of the Brunswick formation, about 3,300 meters above the base of the Triassic. On one of the slabs there is also the imprint of *Otouphebus poolei*. In the same quarry there was also found *Grallator cuneatus* Hitchcock, known from the upper part of the Connecticut Triassic.

Repository.—Academy of Natural Sciences, Philadelphia. Bock Collection. Holotype No. 115219; paratype No. 15223

KINTNERIA BRUNSWICKII Ryan and Willard, 1947
Plate 45, figure 3

Description.—Several tracks from different Triassic localities, covered with numerous, but mostly disconnected foot prints, display this common genus, whose dimensional formula is derived from those found at Gwynedd.

Digit number	I	II	III	IV	V
Digit length, mm.	6	6	10	7	5
Digit angle, degrees	92	31	33	88	
Total width, mm.	11				
Total length, mm.	14				
Step(?), mm.	55				

Digits.—Five digits of pes present. Shape of lower portion linear, terminal sections curved. III digit usually straight and longest,

II curved to the inside, III to the outside. I and V rotated to the rear. Base of digit closely set, forming roundish curve. V digit shortest, retarded. Base of IV digit somewhat below III, and base of II digit adjacent to third, similar to saurischian pes pattern. III digit showing three indistinct pads. No heel pad impressions.

Claws.—Claws sharp, pointed, mostly curved and slightly offset from digit, about 1.8 to 2.0 mm. long, 1 mm. wide.

Functional record.—Gait probably bipedal or hopping, digitigrade or semiplantigrade. Roll-off function similar to that of the saurischians, with middle digit performing final movement solitarily. Rotated digits may have helped in the initial lifting movement, but also suggest arboreal habits, and may also have provided larger support area in a swampy environment.

Discussion.—These small reptile tracks cannot be compared with any other type so far known with the exception of the larger Dinosauria imprints. If we disregard the size, and consider only the three middle toes of our species, we shall be surprised to note that there exists little difference between this imprint and that of *Grallator cuneatus* (pl. 45, fig. 1 and pl. 49, fig. 9). The digit angle, particularly the position of the digit bases and the relationship of the size of the digits to each other, are nearly identical in some instances. Should we add rotated digit I, we have almost an image of *Anchisauripus;* but adding the fifth digit, we may conceive a picture of how the foot of the more primitive dinosaurians functioned. Indeed, it may be plausible to assume that the small reptile which made these tracks was the ancestor of the small Coelurosauria.

The footprints of our species are often found in great numbers on small slabs, without disclosing a locomotive pattern. However, it is believed that these small reptiles did proceed in a hopping manner, as Ryan and Willard (1947) observed several indistinct tracks of similar shape which were oppositely arranged. The type specimen is represented by two obscure tracks on a small slab, of which one is pictured by the same authors (fig. 1), while the more distinct imprint at the margin reveals the structure, which is close to that of those found at Gwynedd. The pointed and curved claws shown in both sets of tracks justify their inclusion in the order of Reptilia.

Location.—The tracks herein described were found in the tunnel deposits at Gwynedd, Pennsylvania, Lockatong formation, Upper Triassic, in the same horizon where *Anchisauripus gwyneddensis* was located, 1,300 meters above the Triassic base. The holotype was found near Kintnersville, Pennsylvania, about 5,800 meters above the base.

Repository.—Academy of Natural Sciences, Philadelphia, Bock Collection. Paratype No. 15220. The Holotype is in the Lehigh University, Bethlehem, Pennsylvania, Paleontological Collection.

DETAILED CORRELATION OF THE TRIASSIC OF EASTERN PENNSYLVANIA AND THE DELAWARE RIVER AREA

Introduction.—Correlation of the Newark Basin rocks has been frequently attempted during the last 100 years. The first estimates placed it with the red beds of the Permian, while other early estimates recognized the upper limits as Jurassic. Gradually, with the disclosure of more paleobiological evidence, the limits have been narrowed, and the age today is generally acknowledged to be Upper Triassic. More specific subdivisions have been occasionally suggested by workers on the different sections, often built on meager data. Inconclusive results were mostly due to (1) the absence of sufficient correlative material, (2) the lack of a comparable type area, and (3) the invariable temptation to use pseudo-evidence, based on the indefinite time value of physical or geological processes, such as separated lava flows, conglomerates, or rock color.

Correlations are fundamentally based on biological synonymy and, in a wider sense, on comparative expressions of faunal and floral evolution. For a true, entire, correlative picture both types of evidence should be used. Differences caused by geographical separation, meteorologic conditions, or ecological background, must be carefully evaluated. Correlative records show that specific similarity in widely separated areas is the exception and generic identification must be employed. The degree of size variations, habits and other close differentia-

tions of the comparative material should be useful. Frequency factors of a population will indicate maximum development, and the association of biological groups should be of paramount value. Therefore, correlations cannot be based on a precise mathematical formula, but they will be adequately represented by the product of qualitative and quantitative comparisons of all the useful paleobiological material available.

The Delaware River area and adjoining sections of the Newark Basin are of particular importance in such a correlation, because it is not only the largest area with easily accessible sections, portraying the complete sequences of sedimentation and formations; but also because it has yielded a large amount of fossil material, of which about 150 faunal and floral species are available for comparison. Depth contour maps, another necessity for proper correlations, have been repeatedly made, the oldest one dating back to B. S. Lyman (1895). The present map (fig. 4), which is used for this correlative analysis, is based on numerous sections measured or calculated in accordance with the principles of vertex monoclines (Bock, in press). The depth contour calculations of the different writers are more or less in agreement.

The presently accepted subdivision of the strata involved recognizes from the base upward, the Stockton, Lockatong and Brunswick formations. The total maximum width of this Triassic belt is 36,000 meters and the calculated maximum thickness of the beds is 7,200 meters. About 3,500 meters have been removed in the past by erosion. On the map (fig. 4) the correlated phases are superimposed on the actual formations of this area, and they extend nearly parallel to the contour lines.

The type sections with which the portions of the Newark Basin are correlated represent those of the equivalent facies of the central European Triassic, which are the best known and paleontologically best developed ones. The classification followed is that of Martin Schmidt (1928, pp. 8–40), who divided the Upper Triassic into lower, middle and upper Keuper.

For those unfamiliar with the corresponding formations, it is briefly stated that the lower Keuper comprises the "Lettenkohle," strata rich in fishes, estherids and plants, and the upper Keuper represents the "Rhaetic," known for its excellent flora and the first mammal teeth.

The middle Keuper, which interests us the most, consists of a number of smaller formations, of which a group of more important ones begins at the base with the "Gipskeuper" known for its huge *Mastodonsaurus*, an amphibian genus, and estherids, followed by the "Schilfsandstein" with many plant species and labyrinthodonts. This is the older portion. The center of the middle Keuper consists of several smaller formations, of which the "Bunte Mergel," "Blasensandstein" and "Coburgsandstein" contain fossils of important phytosaur groups and ganoid fishes. The youngest portion of the middle Keuper represents the well known "Stubensandstein," in which labyrinthodonts and parasuchians flourished. Here, the first group of medium-sized dinosaurs appeared in force. This formation is followed by the "Knollenmergel" famous

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EXPLANATION OF PLATE 49

FIG. *1*—*Gwyneddichnium majore* Bock. Enlarged imprint of pes shown on next plate, fig. 1. (p. 417)

2–4—*Gwyneddichnium minore* Bock. Single pes imprints. ×2. Gwynedd, Pennsylvania. Lockatong formation. Upper Triassic. Holotype. No. 15216. Paratype No. 15217. (p. 419)

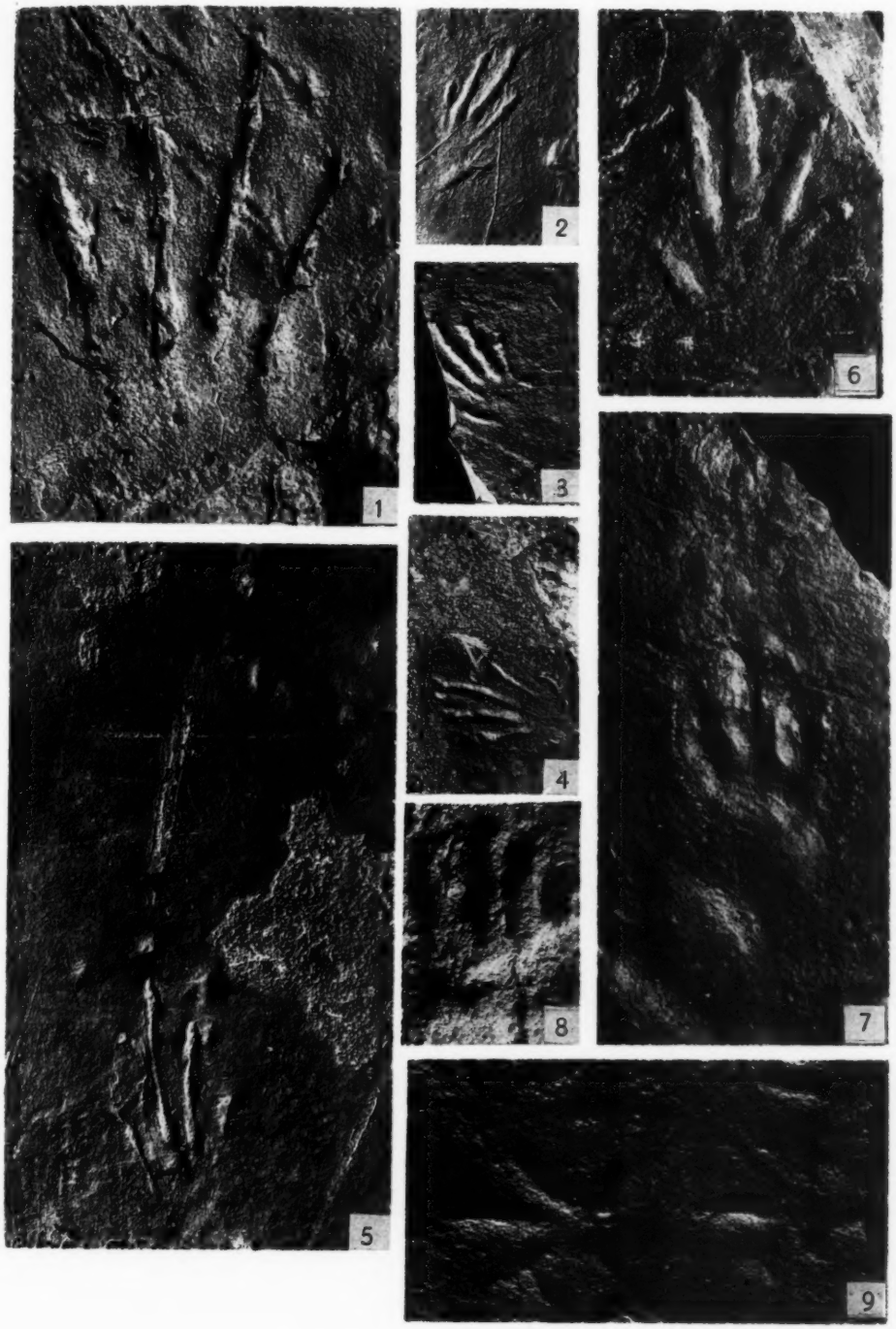
5—*Gwyneddichnium elongatum* Bock. Incomplete track pattern. ×2. Gwynedd, Pennsylvania. Lockatong formation. Upper Triassic. Holotype. No. 15214. (p. 418)

6—Related footprint as shown in Fig. No. 5 from the same horizon. Type No. 15233 (not described) ×2.

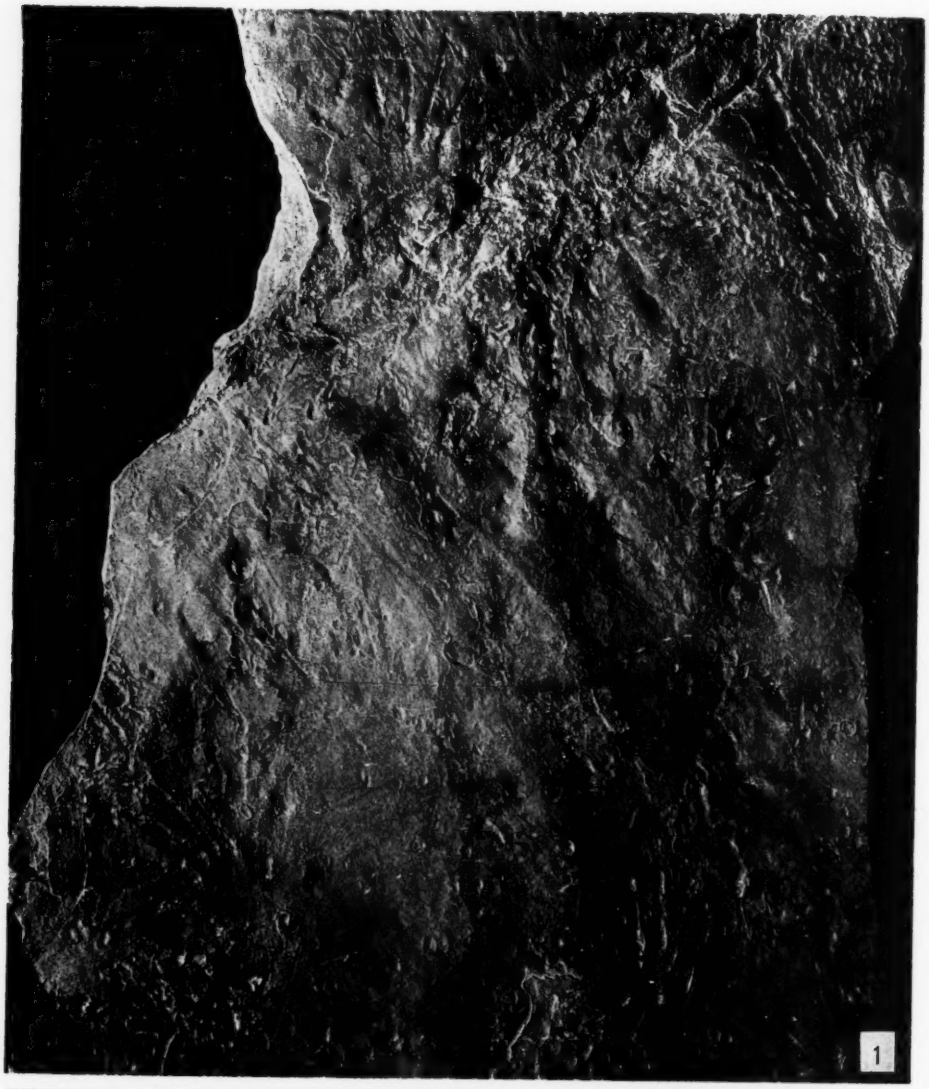
7—*Chirotherium lulli* Bock. Single pes impression and indistinct manus imprint. ×1. Milford, New Jersey. Brunswick formation. Upper Triassic. Holotype. No. S491. (p. 415)

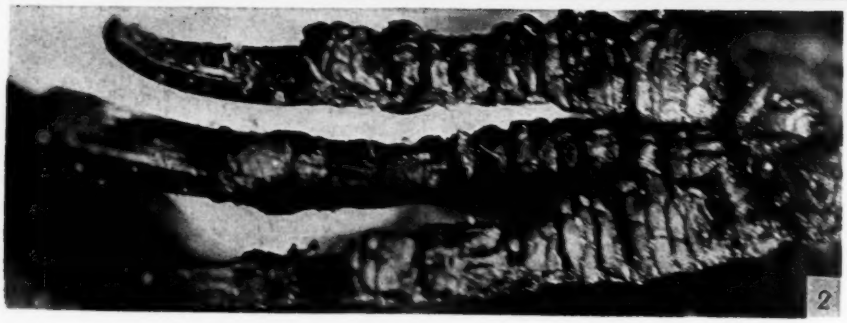
8—Vague impression of track similar to *Chirotherium lulli*, fig. 7 from the same horizon. ×2. Type No. 15241 (not described).

9—*Kintneria brunswicki* Ryan and Willard. Track imprints from Gwynedd, Pennsylvania. Lockatong formation. Upper Triassic. ×2. Paratype. No. 15220. (p. 422)



Bock, Triassic reptile tracks





Bock, Triassic reptile tracks

for its gigantic nonpredaceous *Plateosauria*, one of the largest saurischians of the Triassic. Both formations have yielded only a meager flora.

While the Upper Triassic, with its three Keuper divisions, has produced unsurpassed fossil material in Europe, a few perplexing conditions should be explained. The whole thickness of the German Keuper is only about ten percent of that of the Newark basin. Some of the more important German formations are in certain sections only a few meters thick. Others are intercalated with marine deposits with overlapping marine faunal elements. Floral or faunal material is frequently concentrated in one or the other formation. Between the Schilfsandstein and the Rhaetic a typical flora is missing, although a huge fauna is present. Some groups, such as the crustaceans and numerous plants, indicate a wide vertical distribution. All these difficulties must be taken into account.

The Stockton formation.—Starting with the oldest formation of the Newark Basin, the Stockton beds, we find that the maximum thickness is about 750 meters, consisting of local, narrow, medium-sized border conglomerates, and chiefly coarse to fine grayish-yellow arkosic sandstones grading in the south-eastern section into reddish-brown, hematitic sandstones and shale. The sediments indicate a varying, but rapid, water flow velocity, which does not lend itself readily to good fossil preservation. A few plants near Holicong, Pennsylvania are identified as *Neocalamites* sp., and one single cycadeoid leaf is of middle Keuper character. The foliage of two araucarian conifers found near Ambler and Norristown, Pennsylvania is close to *Widdringtonites keuperianus* (Lettenkohle to Stubensandstein), and the silicified wood from Churchville, Pennsylvania, referred to as *Araucarioxylon vanartsdaleni*, is similar to Keuper types of a rather wide stratigraphic range. Finger-shaped algae (*Dasycladaceae*), which become so abundant in the upper horizons, are occasionally found in the Stockton beds.

The only vertebrate evidence is a portion of a jaw of *Calamops paludosus*, assigned to the labyrinthodonts, although it is rather a primitive phytosaur, close to *Phytosaurus arenaceus* of the Schilfsandstein.

Arthropod tracks near Princeton, New Jersey, assigned to a species of *Limulus*, a genus frequently found in the Lettenkohle and throughout the Keuper, resemble the track pattern of *Psammolimulus göttingensis*. They may have been caused by crustaceans similar to *Gwyneddocarus*, which was found in the lower Lockatong. The most important mollusks unearthed from the Stockton base near Phoenixville, Pennsylvania are *Diplodon yorkensis* and some others, resembling closely *Anodonta arenacea*, of the Kieselsandstein (above the Schilfsandstein).

While the Stockton formation is the weakest link in the correlative chain of the area, the evidence found and evaluated, with the overlying Lockatong fossils, permits assignment to portions of the upper Gipskeuper with overlap in the Schilfsandstein, comprising the early middle Keuper. There exists no convincing evidence to attach any portion of the Stockton to the Lettenkohle facies.

The Lockatong formation.—The Lockatong belt consists chiefly of grayish argillites, interbedded with blackish, well laminated shales, suggesting periodical drainage congestion, favoring microbiological water life. It is known for many remains of the Parasuchia, of which at least two species have been recognized, so far only described as *Clepsisaurus pennsylvanicus*. The species from Belfry, Pennsylvania, consists mainly of a lower, dentated jaw with conical, pointed, fluted, nonserrated teeth and about twice as large frontal grip teeth, While this type is generally recognized to be very close to *Mystriosuchus* from the Stubensandstein, the more recent discovery of similar but

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EXPLANATION OF PLATE 50

FIG. 1—*Gwyneddichnium majore* Bock. Incomplete track pattern of manus and pes impression. Gwynedd, Pennsylvania. Lockatong formation. Upper Triassic. Holotype. No. 15212. (p. 417)

2—Foot of the humming bird *Patagona gigas*. ×10. A.N.S.P. No. 103661.

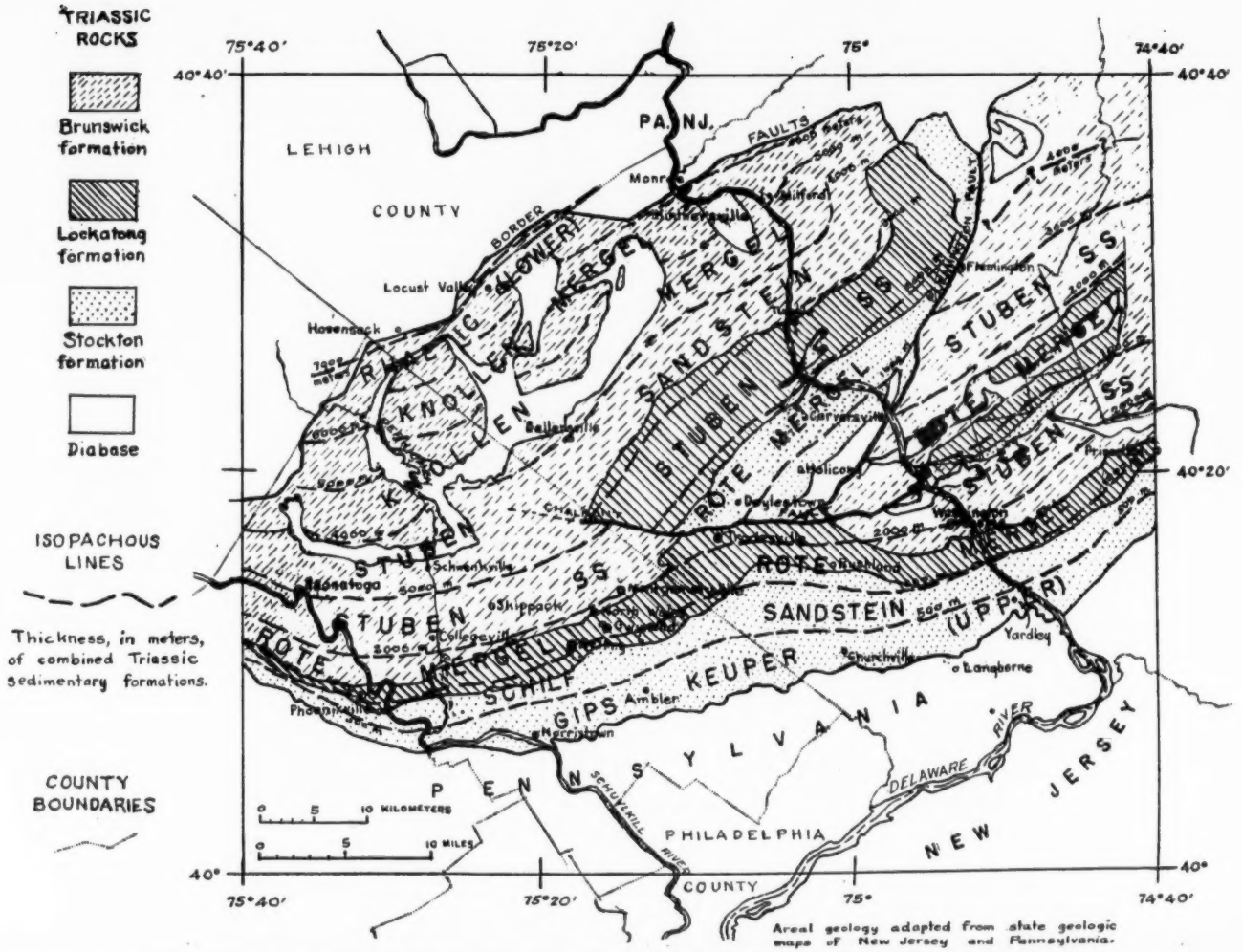

FIG. 4—Geological map with isopachous lines and correlations with European facies, for the Upper

more primitive phytosaurs such as *Francosuchus* in the slightly lower Blasensandstein, makes the position of the Lockatong *Clepsisaurus* somewhat uncertain as they may belong to the *Francosuchus* series. The tiny skeleton of *Gwyneddosaurus* has unfortunately no close or certain contemporary in the Keuper. *Thecodontosaurus gibbidensis* from Phoenixville, represented by a characteristic iguanodon-like tooth, is a nonpredaceous saurischian, also one of the oldest members of this order. Such reptiles appeared first in the Lettenkohle, but they also extend high into the middle Keuper. The unaggressive saurischian track species *Anchisauripus gwyneddensis* may be closely related to *Thecodontosaurus*. The scarcity of the dinosaur material in the Lockatong would rather suggest the age of the Schilfsandstein-Bunte Mergel group than the higher developed Stubensandstein.

The fishes of the Lockatong are typical of this horizon. There are four main groups, *Dictyopyge*, *Redfieldia*, *Semionotus*, *Osteopleurus* and lesser ones. *Dictyopyge macrura* is the most common fish at Gwynedd, resembling closely, with its characteristic, arrowhead-shaped roof scales, *Dictyopyge socialis*, from the Coburg-sandstein. *Redfieldia* is rare in Central Europe, but quite abundant at Gwynedd. *Semionotus fultus* is so far the sole representative of this genus in the lower Lockatong. This fish is also quite close, if not synonymous with, *Semionotus bergeri*, from the Semionotus-sandstein (center of middle Keuper). The most interesting fish is probably the small coelacanth, *Osteopleurus newarki*. It is rare in the southern Lockatong, becoming more numerous at Gwynedd, common at Princeton, and quite abundant at North Bergen, New Jersey, near the Hudson River. This type is often found with a new estherid, soon to be described, and *Candona*, an ostracod, close to *Bairdia procera* from the Lettenkohle and middle Keuper, and occasionally with *Redfieldia redfieldi*, another common ganoid. The little coelacanth has no equivalent in Europe, but it appears to be the most vertically restricted fish, characteristic of the Lockatong belt, which extends with exception of a short interruption from near Phoenixville to above North Bergen. The common presence of *Osteopleurus*, *Candona* and the new estherid with absence or scarcity of *Semionotus*, distinctly separates the Lockatong horizon from the fish beds at Boonton, New Jersey, which are about 2,500 meters higher in the column. Other Lockatong species from Gwynedd are closely related to, or synonymous with *Gyrolepis angulisuculatus*, from the Lettenkohle and *Tetragonalepis* from the Gipskeuper. *Carinacanthus jepseni*, the unique fresh water shark, also found at higher levels north of Montgomeryville, and a species of *Rhapdolepis*, a large coelacanth, with distinct head bones, are all of Upper Triassic character, but not specificially correlative. There is no evidence that the Newark fishes are of Middle Triassic age as suggested by Eastman (1904).

The estherids and ostracods have been already mentioned, showing a wide vertical extension throughout the German Triassic. However, Lea's old species, *Isaura* (*Estheria*, *Pseudoestheria*) *ovata*, which is common from Phoenixville to about the Delaware River, is comparable in size with *Isaura* (*Estheria*) *laxitexta* from the Gipskeuper. The highest horizon of estherids is in the Lockatong-like belt of the Brunswick formation near Sanatoga, Pennsylvania, at a 3,200 meter level, which distinctly proves that the estherids are not confined to the Lockatong formation. Mollusks extend from the Stockton throughout the Lockatong and are represented at Montgomeryville and Carversville, Pennsylvania, by *Diplodon carolus-simpsoni*, *D. wanneri* and *D. yorkensis*. They are close to the unio, *Anodonta arenacea*, Kieselsandstein and *Anodonta dubia*, a middle Keuper type.

The plants of the Lockatong represent a large and varying group, whose types are easily recognized and are correlatively useful, although their average vertical extension is more elastic. The cycadeoids are broadly represented by the medium sized *Pterophyllum powelli*, known from foliage and a whole plant, well matched by *Pterophyllum jaegeri* from the Lettenkohle-Schilfsandstein. At the same location at Carversville *Otozamites brevifolius* and *Pterophyllum braunianum*, both Rhaetic plants, are sparingly found. Associated with these gymnosperms were two species of a somewhat primitive ginkgo, one of which,

Areal geology adapted from state geologic maps of New Jersey and Pennsylvania.

FIG. 4—Geological map with isopachous lines and correlations with European facies, for the Upper

Eoginkgoites sectoralis, is comparable with *Baiera furcata* of the Schilfsandstein, which is, however, more strap-like. The actual palmate foliage has not been reported so far before the Rhaetic. The same beds contained two *Taxus* species, often confused with *Palissya*, as *Taxites* (*Palissya*) *obtusa*, and two short-leafed species of araucarians, one of which, *Cheirolepis latus*, is common throughout the Lockatong, resembling *Widdringtonites keuperianus*, from the Lettenkohle-Stubensandstein. Fine species of *Neocalamites* from Gwynedd and Carversville, somewhat different from *Neocalamites virginiensis*, are equal to *Neocalamites meriana* from the Schilfsandstein. The finger-shaped algae *Dasycladaceae* expanded greatly through the whole formation, forming in places thick layers, but they are of little correlation value, as they appear already in the Permian and in the Muschelkalk, resembling *Gyroporella silesiaca*.

While the Lockatong facies show some extension in the upper and lower border formations of the middle Keuper, mainly shown in the flora, the fishes and reptiles center in beds of Schilfsandstein-Bunte Mergel group age, including a narrow lower portion of the Stubensandstein; but as a whole, the Lockatong represents the central portion of the middle Keuper.

The Brunswick formation.—This formation, mostly consisting of reddish-brown hematitic sandstone and shales, is interrupted by intercalated dark Lockatong-like belts, which become gradually narrower higher in the strata. The beds are about twice as thick as the Lockatong and Stockton combined. Floral and faunal remains, with the exception of finger algae, are scant. However, the fossils at a few strategic localities allow a reasonably accurate correlation. Only two types of reptile remains are known, while other evidence consists of reptilian tracks. Just above the Lockatong strata, near the 3,000 meter contour line, a narrow belt stretching from Sanatoga, passing north of Collegeville and Schwenkville, to Tumble Falls on the Delaware River, reveals at these four localities the footprints of medium-sized, probably predaceous Saurischia, which have been identified as *Grallator cuneatus*, *Grallator tenuis* and *Anchisauripus sillimanni*. They may be correlated with similar sized species of *Halticosaurus*, and *Procompsognathus triassicus* of Stubensandstein age. At the opposite end, beyond the Delaware River, in the neighborhood of Flemington, New Jersey, the small armored pseudosuchian *Stegomus arcuatus jerseyensis*, was found, which compares favorably with *Aetosaurus crassicauda* from the Stubensandstein, although both genera are distinct in some minor details. The Flemington level is about 3,400 meters. The next higher horizon at Milford, New Jersey, on the Delaware River has yielded the large tracks of *Chirotherium parvum* and *Chirotherium copei*. They measure up with the *Chirotherium* tracks shown by Kuhn (1936) from the Blasensandstein. The saurischian tracks of this horizon are not of the gigantic type, but include medium-sized species of *Grallator* and the large *Sauropus barratti*, which may be related to the Ornithischia. The large track of the nonpredaceous *Gigandipus caudatus*, of Turners Falls, Massachusetts or *Eubrontes giganteus*, are still missing at Milford; however, the latter and numerous others are present in the somewhat lower horizon at Whitehall, New Jersey, which locality shows a good replica of the Turners Falls track species. These large-sized saurischians are widely spread throughout the German Knollenmergel, where they must have reached their zenith, as they considerably decline in number in the Rhaetic, perhaps because of some ecological conditions. One of the larger ones, *Pachysaurus wetzelianus*, from the Knollenmergel, fits closely into the track of *Eubrontes giganteus*, known from Whitehall and Turners Falls. About 1,900 meters higher, near Hosensack, Pennsylvania, close to the upper level of the basin, the type specimen of *Clepsisaurus pennsylvanicus* was discovered in coarse, pinkish sandstone. Many bones, including vertebrae and two teeth, give a good paleontological record, but some controversial gaps remain. The teeth are fundamentally different from those of the *Clepsisaurus* species from Belfry, Pennsylvania, in shape and microscopic surface features. The specimen of the lower strata can be closely compared with *Mystriosuchus planirostris* although similarity with *Francosuchus* is a possibility. However, the teeth of the Hosensack

type resemble more those of *Angisthorinopsis* of the Rhaetic, although there is otherwise little difference between the latter and *Mystriosuchus*. As the *Clepsisaurus* from Hosensack occurs about 5,900 meters higher in the profile than the jaw from Belfry, and as it is above the Milford Knollenmergel facies, it could be reasonably expected that the existing, though small, differences are the reflection of an advanced time interval.

The flora of the Brunswick beds is abundantly represented by dasycladacean algae in many of its hematitic layers. In a dark belt near Sellersville, Pennsylvania, near the 4,000 meter level, the foliage of a cycadeoid, described as *Brunswickia dubia* corresponds with *Pterophyllum carnallianum*, from the Rhaetic. At Milford, New Jersey, in the *Chirotherium* horizon, an extensiye floral layer was recently discovered, showing the important fern *Clathropteris platyphylla*, and the conifer *Cheirolepis münsteri*, both prominent in the German Rhaetic, a new large-leafed araucarian, which is only known elsewhere from Turners Falls, Massachusetts, and a more highly developed entire-leafed ginkgo, *Ginkgoides milfordensis*, which is close to *G. obovata* of Rhaetic age. It probably is not a connecting link with the palmate ginkgos from the lower Carversville level.

The Brunswick paleobiological picture displays in the lower strata a homogeneity which indicates with reasonable certainty that the 3,000 meter contour area with its medium-sized dinosauria is of Stubensandstein age. The Knollenmergel is assigned to the 4,000 to 6,000 meter level on account of the Milford plant and track fossils, which are somewhat in the center of the belt. They are definitely of more advanced development than the strata below. Above the 6,000 meter level, which includes the type specimen of *Clepsisaurus*, the beginning of the Rhaetic is to be expected. The Rhaetic aspect of the plants in the strata assigned to the Knollenmergel is considered to be an early overlap.

Conclusions.—The Triassic of the Delaware River area and adjoining sections, occupies, as a whole, the position of the Central European middle Keuper. The oldest beds, comprising the Stockton formation, correspond with those of the late Gipskeuper facies with overlap in the Schilfsandstein, representing a rather short period. The following strata, those of the Lockatong formation, which covered a considerably longer period, due to its nature of deposition, represent consecutively the Schilfsandstein-Bunte Mergel series with some overlap in the Stubensandstein, comprising about the central portion of the Middle Keuper. The Brunswick formation, with its extensive red-brown hematitic beds, extends from the Stubensandstein to the Knollenmergel, the upper portion of the middle Keuper. A narrow, laterally restricted belt extends into the level of the early Rhaetic. While the latter is absent in most groups of the Newark Basin, it should also be remembered that a large portion of the higher Triassic strata, due to its geological structure, has been removed by erosion. These beds must have certainly extended into upper Keuper levels.

It is proposed to consider this area, due to its strategic position, geological extent, and fossils, as a correlative type section in regard to the Newark Basin, in its entirety, in order to arrive at dependable correlative data for its remaining portions. The Central European Triassic must continue to be looked upon as the basic type area.

CORRELATIVE REFLECTIONS ON OTHER EASTERN TRIASSIC AREAS

The adjacent New Jersey Triassic would cause little difficulty in its correlation, developed on the base of depth contour lines, as the upper and lower stratigraphic limits in the area are already reasonably accurately defined. A correlative connecting link of the type area with that of the lower portion in New Jersey is formed by the small Coelacanth-Estherid-*Candona* horizon, typical for the Lockatong formation of Schilfsandstein-Rote Mergel age, stretching toward the Hudson River, while the age of the uppermost layers is limited by the formidable evidence of the medium, and particularly the large, dinosaurian tracks correlated with the Knollenmergel.

The Triassic deposits of the Connecticut Valley are much less adaptable for precise subcorrelations on account of the numerous diastrophic disturbances, such as the oc-

currence of extensive lava beds and faulting. However, the uppermost horizon displays so clearly and insistently a similar saurischian track assembly to those of the New Jersey horizons at Whitehall and Milford, also found at York Springs, Pennsylvania, and Aldine, Virginia, that the whole upper border beds of this large Triassic section should be assigned to the same age, the Knollenmergel series. More complicated is the comparison of the base in the Connecticut Valley, which with a more highly developed and abundant *Semionotus* population and still quite large dinosaurian evidence, including *Stegomus arcuatus*, does not seem to extend into the lower *Osteopleurus*-Estherid-Ostracod strata of the Lockatong. Judging from the material available, it should be concluded that the Triassic of the Connecticut Valley comprises the facies of the Stubensandstein to the Knollenmergel with overlap in the central portion of the middle Keuper, but that the lower facies of the middle Keuper are wanting.

The Triassic of the Susquehanna River area offers an excellent correlative horizon near Goldboro, Pennsylvania with four species of medium-sized *Grallator* tracks, identifying it with the lower Brunswick horizon (Stubensandstein) and a large dinosaurian track species from near York Springs, Pennsylvania, belonging to the uppermost horizon of the Newark Basin (Knollenmergel). The basal beds of the Susquehanna Triassic extend in age only slightly into the higher levels of the Lockatong, to judge from the evidence of the fish population, although mollusks and estherids are sparingly present.

Another identical horizon, of uppermost Brunswick age, has been discovered at Aldine, Virginia, where *Eubrontes giganteus* and a host of medium and larger species of *Grallator*, as well as the fern, *Clathropteris*, were found.

In the Richmond, Virginia, coal basin, the lower beds, represented in Pennsylvania by the Lockatong formation, are missing altogether. The unsurpassed flora of the coal belt, which comprises 55 different species, matches that of the Stubensandstein and Knollenmergel. Three estherid species are also fundamentally different from those of the Lockatong phyllopods.

In the North Carolina region, the coal beds of the Cumnock formation again represent the Lockatong facies with essentially the same fauna, the Coelacanth-Estheria-*Candona* assemblage.

From these comparative, though incomplete, findings, which it is hoped, will soon cover the whole Newark basin in more detail, it may be deduced that no general formula can be applied for the different sections of the eastern Triassic. The establishment of its correlative age must be strictly built on the evidence presented by their faunas and floras. However, none of the different areas, stretching from Nova Scotia to North Carolina, discloses any paleontological data, which do not, as a whole, agree with the facies of the European middle Keuper.

DURATION OF THE NEWARK BASIN

After a close correlation of the Triassic beds of the Delaware River region and adjacent sections has been completed, another much more indefinite problem, the determination of the time required for laying down this huge mass of sediments, should be approached. While the deposition of the total European Triassic has been generally recognized as having required approximately 30 million years, of which half was taken up by the deposition of the Upper Triassic beds, more accurate figures, which could be obtained from radium dissemination tests, have not been so far secured, and, therefore, the above estimated figure is adapted here as a base, with all the errors involved. Middle Keuper time is believed to have been as long as lower and upper Keuper time together, which would be about 7.5 million years. Ignoring the short Rhaetic segment at the top of this Triassic area, and allowing a proportional deduction at the beginning of the middle Keuper, the sediments of this section of the Newark Basin are estimated to have been laid down within 6.5 million years.

From comparative studies of the velocity and nature of sedimentation, which is different for all three formations, and from a close examination of the distribution of fossils and development of paleontological phases, the Stockton formation, with its fast cycle sedimentation, is postulated to

have lasted one million years; the Lockatong formation, with its low velocity lake sedimentation 2 million years, and the Brunswick formation with its shallow flood bed and medium velocity cycles, about 3.5 million years. This amounts to an average of about 1 mm. of sedimentation per year. Of course, these figures can not be any more accurate than the postulation of the age of the whole period, and they must remain strictly as an estimate. However, they provide a reasonable picture of the duration of this Triassic section, which is considerably shorter than has generally been believed. It also affords an approximate time scale for the evolutionary development of the different groups of Triassic plants and animals.

The following schedule shows the most important correlative material, grouped with the formations, localities and European facies.

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Formation		Thickness meters	Location	Duration	Correlated facies	Correlative fossils
		Triassic Top				
UPPER KEUPER	BRUNSWICK	7000	Hosensack	3.5 Million years	RHAETIC	*Clepsisaurus pennsylvanicus.*
		6000	Monroe		KNOLLEN-MERGEL	*Clathropteris, Cheirolepis münsteri. Ginkgoites milfordensis* association. *Chirotherium parvum. Sauropus barratti. Eubrontes giganteus. Grallator cuneatus.*
		5000	Milford (Whitehall)			
		4000	Sellersville		STUBEN-SAND-STEIN	*Brunswickia dubia.*
		3000	Flemington Sanatoga Collegeville Schwenkville Tumble			*Stegomus arcuatus jerseyensis. Grallator cuneatus. G. tenuis Anchisauripus sillimanni.*
MIDDLE KEUPER	LOCKATONG	2000	Tradesville Montgomeryville Carversville Gwynedd, Belfry	2 Mill. years	COBURG SS BLASEN SS BUNTE-MERGEL	*Dictyopyge macrura. Semionotus fultus. Mystriosuchus.* (*Francosuchus.*) *Redfieldia redfieldi. Cheirolepis latus. Pterophyllum powelli, P. jaegeri.*
	STOCKTON	1000	Princeton Phoenixville Ambler Holicong Churchville	1 Mill. years	SCHILF SANDSTEIN GIPS-	*Neocalamites. Widdringtonites Equisetites sectoralis* association. *Osteopleurus-Estherid-Ostracod* association *Thecodontosaurus. Diplodon yorkensis.*
		TRIASSIC BASE				
LOWER KEUPER					KEUPER LETTEN-KOHLE	*Gyrolepis angulissulcatus.*

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JOURNAL OF PALEONTOLOGY, VOL. 26, NO. 3, PP. 434–451, PLS. 51–54, MAY 1952

REVISION OF THE NORTH AMERICAN TRILOBITES OF THE FAMILY EODISCIDAE

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ABSTRACT—The eodiscid trilobites are divided into two families, the Pagetiidae comprising all the forms with eyes and facial sutures, and the Eodiscidae including the sutureless, blind forms. The present revision of the North American Eodiscidae is based upon study of the type material of all the described forms, many of which are properly illustrated for the first time. After elimination of forms that do not belong in the family and of several invalid genera and species, there remain only five genera and 12 species of North American Eodiscidae. The recognized genera are *Calodiscus*, *Serrodiscus* and *Weymouthia* of the Lower Cambrian and *Dawsonia* and *Eodiscus* of the Middle Cambrian. The nomenclature, taxonomy and geographic distribution of the group are briefly discussed.

INTRODUCTION AND ACKNOWLEDGMENTS

THE compilation of a section of the new Treatise on Invertebrate Paleontology led the writer to a nomenclatural and taxonomic revision of the eodiscid trilobites. Since several of the described species were never properly illustrated and some are poorly understood, it was deemed advisable to publish the present revision of the family Eodiscidae, where all the North American forms so far brought to light are discussed and illustrated by photographs. The reason for limiting this study to North America is that the writer had no access to the types of most of the European, Asiatic and Australian forms, which, on the other hand, have mostly been well described and illustrated by authors who were familiar with the fossils and their occurrence.

Within the last ten years, the eodiscids were discussed, among others, by Lermontova (1940), R. and E. Richter (1941), Kobayashi (1943a, 1943b, 1944), Westergård (1946) and the writer (Rasetti, 1948a, 1948b). Kobayashi's papers are the only ones that deal with the entire group, including its nomenclature, phylogeny, classification, stratigraphic and geographic distribution. Unfortunately, Kobayashi did not have at his disposal most of the European and American material, hence his judgment of many species was based on old, inaccurate descriptions and illustrations. Errors arising from this source and (in the writer's opinion) an excessive fragmentation of the families and genera, considerably decrease the value of his work.

All the available types and other specimens of North American eodiscids known to the writer were examined. This was made possible by the cooperation of several institutions. The writer gratefully acknowledges his indebtedness to the following persons: Dr. G. Arthur Cooper, U. S. National Museum; Dr. Madeleine A. Fritz, Royal Ontario Museum of Palaeontology; Dr. Winifred Goldring, New York State Museum; Dr. B. F. Howell, Princeton University; Dr. N. D. Newell, American Museum of Natural History; and Dr. J. W. Wells, Cornell University.

STRUCTURE OF THE EODISCID SHIELD

Kobayashi (1944) gave a good detailed description of the eodiscid shield, hence only a brief summary of the essential characters is included.

Cephalon.—Approximately semicircular or semielliptical, moderately to strongly convex as a whole. Dorsal furrow strong to almost completely obliterated (*Weymouthia*). Glabella subcylindrical to subconical, rarely expanded in the frontal lobe (latter feature known only in small individuals that may represent immature stages). Glabellar furrows shallow or obsolete. Occipital furrow of variable depth; occipital ring sometimes extended into a strong occipital spine. Area in front of the glabella usually depressed, but never showing such a narrow, well-delimited furrow as the preglabellar furrow of the agnostids. Cheeks

mostly convex and in some forms considerably elevated in their posterior portion. Rim developed all around the cephalon, in certain forms greatly expanded mesially. A characteristic feature of the eodiscids is the tendency to develop tubercles, crenulations or radial impressions on the cephalic rim.

The blind forms do not possess dorsal cephalic sutures and the presence of a doublure of approximately even width, forming one piece with the dorsal portion of the shield, indicates that there are no facial sutures of any kind. Nevertheless, Beecher and Raymond, by classifying these trilobites under the order Hypoparia, implicitly assumed the presence of ventral free cheeks, whose existence has never been demonstrated. Apparently there is no published evidence for the existence of a hypostoma in the eodiscids.

In the oculate forms, there exist facial sutures and free cheeks. Both branches of the facial suture are short, running almost directly to the margin of the head from the respective ends of the palpebral lobe. The latter is more or less well defined by a palpebral furrow, and is always small; the ocular ridges may be indicated. Genal spines are absent or inconspicuous.

Thorax.—The thorax consists of 2 or 3 simple segments. The axial rings never show the peculiar, paired tubercles usual in the agnostids. Pleura never extend into spines. In certain species (*Dawsonia dawsoni*, *Pagetia bootes*) the extremity of the first pleuron points backward, while that of the second pleuron points forward. The same is true of the first and third pleura in *Eodiscus*. Evidently this structure favors enrollment of the shield. Enrolled specimens are known in *Serrodiscus speciosus* and *Dipharus cobboldi*. Probably all eodiscids possessed the faculty of enrollment.

Pygidium.—About as large as the cephalon and of similar proportions, semicircular to subtriangular. Axis usually well defined and elevated (except in *Weymouthia*), generally occupying most of the pygidial length, composed of a highly variable number of segments (notice the great difference from the agnostids in this character). From five to 14 segments, including the terminal section, were observed. Pleural lobes convex, furrowed or smooth. Marginal furrow and narrow rim well defined even in the smoothest forms. There is a terminal axial spine in *Pagetia*. The margin is usually smooth, but in *Serrodiscus* and in the type species of *Calodiscus* there is a series of short marginal spines.

Surface ornamentation.—The test of some eodiscids appears smooth, in others the surface is punctate or granulated, apart from the already mentioned ornamentation of the cephalic rim.

GEOGRAPHIC AND STRATIGRAPHIC DISTRIBUTION

The Eodiscida are confined to Lower and Middle Cambrian strata. Owing to the uncertainty of correlation of the Lower Cambrian formations in different areas, it is difficult to state what is the earliest occurrence of the eodiscids. In the Acado-Baltic province, eodiscids appear in the Lower Cambrian of England, Poland, Silesia, Sweden, Norway, Spain, Portugal, Newfoundland and Massachusetts. Most of these Lower Cambrian forms are sutureless, but *Dipharus* (=*Hebediscus*) a genus with eyes and facial sutures, is known from the Lower Cambrian of England, Newfoundland and Massachusetts. In the Appalachian province, Eodiscida also appear in the Lower Cambrian both with blind and oculate genera. Blind forms are almost exclusively known from the Schodack formation of New York, while oculate species occur in the Parker shale of Vermont, the conglomerate boulders of the St. Lawrence valley, and also in the Schodack. There is insufficient evidence to decide whether the oculate or blind forms appear first. In the Cordilleran province blind eodiscids are unknown, while oculate forms (*Pagetia*) already appear in *Olenellus*-bearing strata and become common in the Middle Cambrian.

Middle Cambrian eodiscids are known from Europe, Asia, Australia and North America. The deposits of the Acado-Baltic province (England, France, Sweden, eastern Newfoundland and New Brunswick) yielded only sutureless forms, represented by great numbers of individuals in certain shaly beds. Deposits of the Appalachian and Cordilleran provinces yielded only the oculate genus *Pagetia*. This is also known

from India, Korea and Australia. According to Kobayashi (1944) the Middle Cambrian of Korea also contains blind forms. Lermontova (1940) described several genera of the Pagetiidae from the Lower and Middle Cambrian of Siberia.

The latest known occurrence of an eodiscid is probably that of *Opsidiscus bilobatus* (Westergård, 1946) from the *Leiopyge laevigata* zone of Sweden. The latest occurrence of an oculate eodiscid, at least in North America, is that of *Pagetia* in the upper Stephen formation (*Bathyuriscus-Elrathina* zone) of British Columbia.

It would be difficult at the present stage of knowledge of the succession of Cambrian deposits to arrange the Lower Cambrian eodiscids discussed in this paper in chronological order. For example, we do not know whether the Hoppin limestone of Massachusetts and the equivalent formations of eastern Newfoundland are younger or older than the Schodack limestone at Troy, New York, as the first belong to the deposits of the Acado-Baltic province, the latter to the Appalachian province. Although the faunas of these two provinces are markedly different, the Lower Cambrian eodiscids are closely related and there may be even species in common. No such relationship subsists in the Middle Cambrian.

More detailed ranges of the genera are given with the systematic descriptions.

NOMENCLATURE

It seems necessary to review the essential nomenclatural history of the group since neither R. and E. Richter (1941) nor Kobayashi (1943a, 1943b, 1944) gave entirely exhaustive discussions of the problems involved.

Following Salter, most of the eodiscids described until 1913 were referred to *Microdiscus* Emmons, 1855, although the authors were well aware of the fact that the type of that genus was not an eodiscid.

Dawson (1868) in describing new species credited to Hartt listed *Microdiscus dawsoni* Hartt MS adding the following comment: "Mr. Hartt had originally described this species under the new generic name of *Dawsonia;* but Mr. Billings regards it as a species of *Microdiscus* of Salter." The name *Dawsonia* was recognized by Matthew (1896a, 1896b) as a subgenus of *Microdiscus*, disregarded by later authors, and recently resurrected by Resser (1937) who considered the above-quoted text as a valid designation

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Explanation of Plate 51

The test is preserved in all figured specimens.

Figs. *1–11*—*Calodiscus lobatus* (Hall). *1*, Cephalon figured by Walcott, ×12; USNM 15394, plesiotype. *2*, *3*, Dorsal and lateral views of pygidium figured by Walcott, ×12; USNM 15394, plesiotype. *4*, *5*, Dorsal and lateral views of cephalon collected by the writer, ×12; USNM 116361, plesiotype. *6–8*, Dorsal, lateral and frontal views of cephalon, ×8; AMNH 210, syntype. *9*, Another cephalon, ×8; AMNH 210, syntype. *10*, *11*, Dorsal and lateral views of pygidium, ×8; AMNH 210, syntype. All specimens from conglomeratic limestone of the Schodack formation in ridge in eastern suburb of the city of Troy, New York (USNM locality 27). (p. 441)

12–16—*Calodiscus agnostoides* (Kobayashi). *12*, *13*, Dorsal and lateral views of cephalon figured by Walcott, ×12; USNM 116356, holotype; locality USNM 27. *14*, Cephalon, ×12; USNM 116358, plesiotype; locality USNM 33b. *15*, Small cephalon, ×12; USNM 116359, plesiotype; locality USNM 36a. *16*, Cephalon, ×12; USNM 116357, plesiotype; locality USNM 33. All specimens from limestone of the Schodack formation; for localities see text. (p. 442)

17, *18*—*Calodiscus* cf. *agnostoides* (Kobayashi). Dorsal and lateral views of cephalon, ×8; USNM 116360. Locality USNM 43a: 1 mile ENE of Salem, Washington County, New York. (p. 443)

19–21—*Calodiscus meeki* (Ford). Dorsal, lateral and frontal views of cephalon, ×8; NYSM 4587, holotype. From conglomeratic limestone of the Schodack formation in ridge in eastern suburb of the city of Troy, New York. (p. 442)

22–27—*Calodiscus schucherti* (Matthew), ×6. *22*, *23*, Dorsal and lateral views of cephalon. *24*, *25*, Lateral and dorsal views of pygidium. *26*, Cephalon. *27*, Pygidium; ROM 138, syntypes. From limestone of the Schodack formation in ridge in eastern suburb of the city of Troy, New York. (p. 441)

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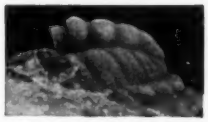
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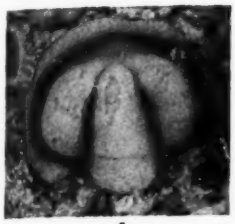
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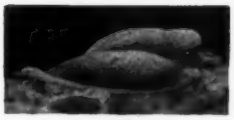
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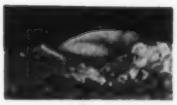
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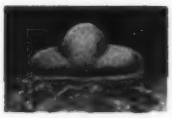
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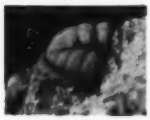
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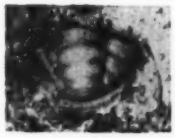
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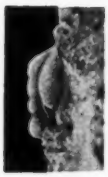
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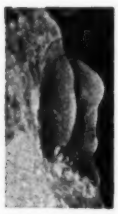
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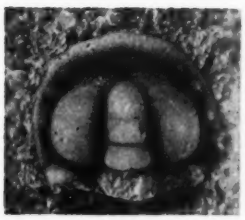
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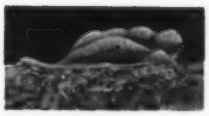
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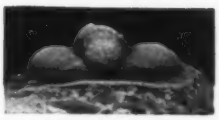
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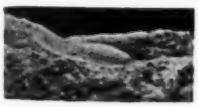
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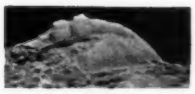
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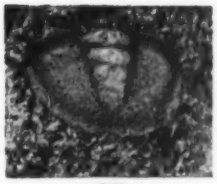
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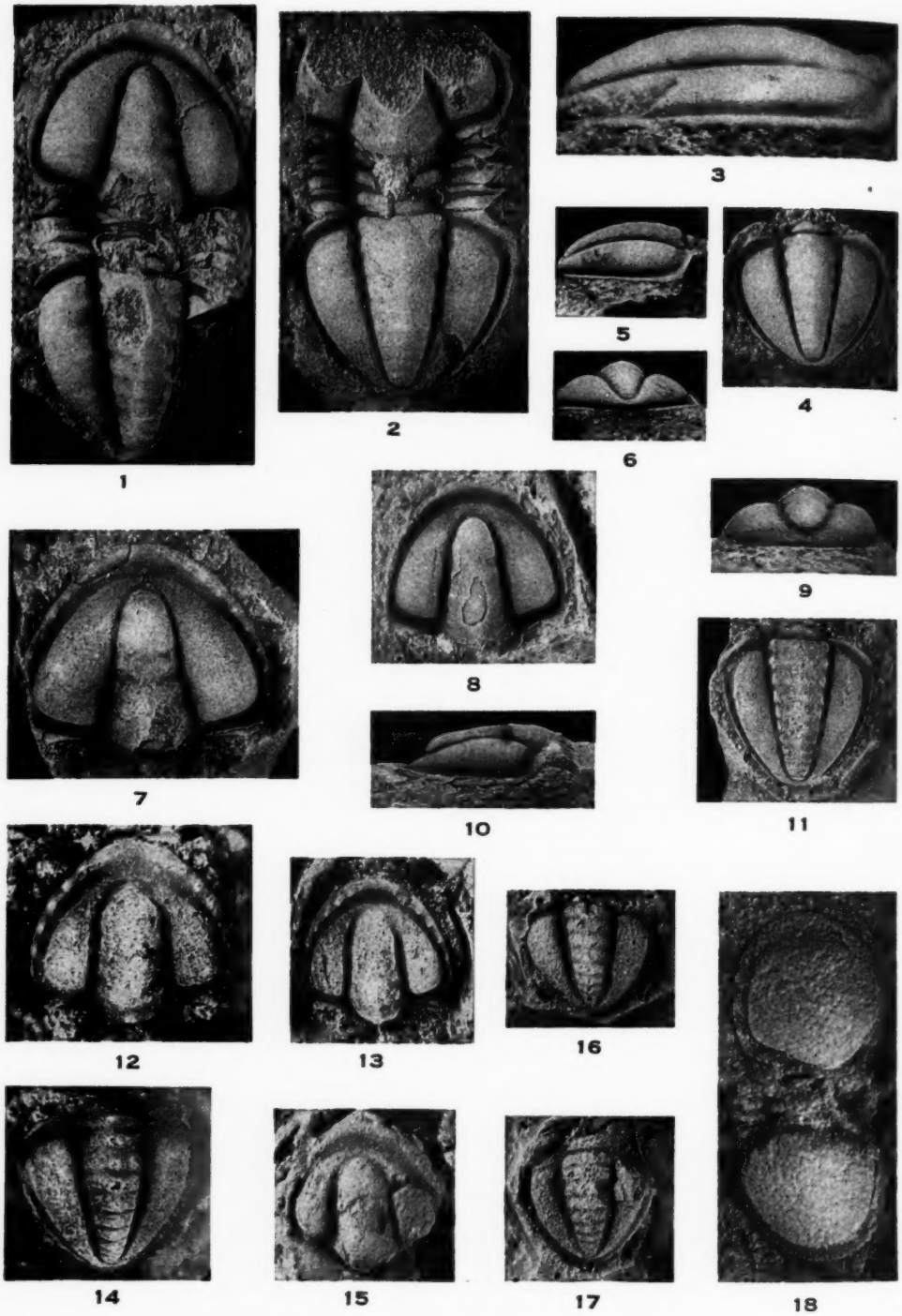
Rasetti, eodiscid trilobites



Rasetti, eodiscid trilobites

of the generic name and of the type species (by monotypy). This conclusion was strongly opposed by R. and E. Richter (1941). After consideration of Article 25 of the Rules of Nomenclature and of Opinion 4 of the ICZN, the writer is unable to see the validity of R. and E. Richter's contention that *Dawsonia* is not available because it was rejected by the author (Hartt) and published against his will by Dawson. The text does not indicate that Hartt rejected the name *Dawsonia;* it was Dawson who, on Billings' advice, referred the species to *Microdiscus*. Hence the writer recognizes *Dawsonia* Hartt in Dawson, 1868, as an available generic name for eodiscid trilobites. Kobayashi (1944) not only recognized *Dawsonia* but erected the family Dawsoniidae and the superfamily Dawsoniidea.

The generic name *Eodiscus* has a history similar to that of *Dawsonia*, being rejected by the author responsible for its first publication. Walcott (1884) discussing the species *Microdiscus punctatus* Salter, added the following comment: "Mr. Hartt evidently intended to describe it, as the name is given in his list, and selected specimens were mounted on blocks, one of which bears the name *Eodiscus pulchellus* Hartt, n. gen., n. sp." Recent authors, with the exception of Lake (1946) ignored Walcott's publication of the name *Eodiscus* in 1884 and credited the name to Matthew, 1896. Walcott's publication is evidently as valid as Dawson's publication of *Dawsonia* for the identical reasons. The writer recognizes *Eodiscus* Hartt in Walcott, 1884, as an available generic name for eodiscid trilobites, with the type species (by monotypy) *Eodiscus pulchellus* Hartt in Walcott, 1884 (= *Microdiscus scanicus* Linnarsson, 1883).

Matthew (1896a, 1896b) discussed the classification of the eodiscids. He placed all the species under the genus *Microdiscus*, divided into four sections, two of which were designated by the subgeneric names *Dawsonia* Hartt, 1868 and *Eodiscus* Hartt, 1884, while the other two remained unnamed.

Raymond (1913) reviewed the taxonomy of all the eodiscids known at that time. He pointed out that the use of *Microdiscus* for eodiscids was illegitimate, and suggested that all the species be distributed among three genera: *Eodiscus* Matthew, 1896, *Goniodiscus* Raymond, 1913, and *Weymouthia* Raymond, 1913, with the respective types *Microdiscus schucherti* Matthew, 1896, *Agnostus lobatus* Hall, 1847, and *Agnostus? nobilis* Ford, 1872. Thus Raymond considered invalid the publication of *Dawsonia* by Dawson in 1868 and that of *Eodiscus* by Walcott in 1884, in the latter case designating the type species in contradiction with the one already established by Walcott by monotypy.

Walcott (1916) described a genus of eodiscids with eyes and facial sutures, *Pagetia*, with the type species *Pagetia bootes* Walcott.

EXPLANATION OF PLATE 52

FIGS. *1–11—Serrodiscus speciosus* (Ford). *1*, Shield whose cephalon was figured by Ford, ×4; NYSM 4588, lectotype. *2*, Shield with part of the cephalon broken off, figured by Walcott, ×4; NYSM 4590, plesiotype. *3*, Side view of pygidium of same specimen, showing marginal spines, ×8. *4–6*, Dorsal, lateral and posterior views of pygidium, ×4; NYSM 4589, paratype. The specimens illustrated in figs. *1–6* preserve the test and were collected from limestone of the Schodack formation in ridge in the eastern suburb of the city of Troy, New York. *7*, Cephalon, ×3; USNM 17478, plesiotype. *8–10*, Dorsal, frontal and lateral views of cephalon, ×3; USNM 17478, plesiotype. *11*, Pygidium, ×3; USNM 17478, plesiotype. The specimens illustrated in figs. *7–11* were figured by Walcott and preserve the test. Locality USNM 37: limestone of the Schodack formation 1.5 miles south of Salem, Washington County, New York. (p. 444)

12–17—Serrodiscus bellimarginatus (Shaler & Foerste). *12*, *13*, Cephala, ×5; USNM 18329, plesiotypes. *14*, Pygidium, ×5; USNM 18329, plesiotype. The specimens illustrated in figs. *12–14* are internal casts and were collected from USNM locality 41, 600 meters west of Manuels Brook, Conception Bay, Newfoundland. *15*, Cephalon, ×5; ROM 145. *16*, *17*, Pygidia, ×5; ROM 750. The specimens illustrated in figs. *15–17* (internal casts) are syntypes of *Microdiscus bellimarginatus insularis;* locality same as preceding. (p. 445)

18—Weymouthia nobilis (Ford). Shield lacking the test, ×8; MCZ 246, plesiotype. From the Weymouth formation at Weymouth, Massachusetts. (p. 446)

Vogdes (1917) erected the genus *Delgadoia* with the type species *Microdiscus caudatus* Delgado.

Clark (1923) described a larval form, now believed to represent an eodiscid, as *Dipharus insperatus*, n. gen., n. sp.

Howell (1935) remarked that Raymond's name *Goniodiscus* was preoccupied and replaced it with *Calodiscus*.

Whitehouse (1936) erected the genus *Hebediscus* with the type species *Ptychoparia attleborensis* Shaler and Foerste.

Lermontova (1940) described five new genera of eodiscids assigned to the family Pagetiidae: *Cobboldia* (type *Cobboldia dentata* Lermontova), *Glabrella* (type *Glabrella ventrosa* Lermontova), *Pagetiellus* (type *Microdiscus lenaicus* Toll), *Pagetina* (type *Pagetina rjonsnitzkii* Lermontova), and *Triangulaspis* (type *Ptychoparia meglitzkii* Toll). A critical analysis of Lermontova's work by R. and E. Richter (1942) points out that probably *Glabrella* and *Triangulaspis* are not eodiscids. *Pagetina* would deserve recognition if the genotype had three thoracic segments, which according to Lermontova is possible but not proven. *Pagetiellus* and *Cobboldia* appear to be valid genera. The writer does not know any North American forms referable to either.[1]

R. and E. Richter (1941) recognized a single genus of blind eodiscids (in addition to the oculate forms *Pagetia* and *Hebediscus*) for which they used the name *Eodiscus* Matthew, 1896, with the type species *Microdiscus schucherti* Matthew. It was shown above that *Eodiscus* was first published by Hartt in Walcott, 1884, and that the type species was established at the same time. R. and E. Richter accepted as subgenera *Eodiscus* s. str., *Weymouthia* Raymond, and *Serrodiscus* R. and E. Richter, 1941, with the type species *Eodiscus* (*Serrodiscus*) *serratus* R. and E. Richter.

Kobayashi (1943a, 1943b, 1944) admitted no less than 17 eodiscid genera and subgenera (not including those erected by Lermontova, with whose work he evidently was not acquainted), nine of which were new, distributed in five families and six subfamilies. Apart from the excessive fragmentation of the taxonomic units, Kobayashi's attempted revision suffers from the shortcomings of paleontologic work based on perusal of the old literature rather than on study of actual fossils. His new genera are: *Cobboldites* (type *Microdiscus comleyensis* Cobbold), *Paradiscus* (type *Microdiscus speciosus* Ford), *Metadiscus* (type *Microdiscus sculptus* Hicks), *Spinodiscus* (type *Microdiscus punctatus* Salter), *Brevidiscus* (type *Brevidiscus lunulatus* Kobayashi), *Deltadiscus* (type *Microdiscus punctatus precursor* Matthew), *Eopagetia* (type *Microdiscus significans* Etheridge), *Mesopagetia* (type *Pagetia clytia* Walcott), and *Alemtejoia* (type *Microdiscus souzai* Delgado). *Eopagetia* and *Mesopagetia* are considered subgenera of *Pagetia*.

Of these genera, *Cobboldites* and *Metadiscus* may be valid, but as no American forms seem referable to them, they are not further discussed here. *Paradiscus* is a subjective synonym of *Serrodiscus*, which has priority. *Spinodiscus* is a subjective synonym of *Eodiscus*. *Brevidiscus* has the same type species as *Calodiscus*, although redescribed by Kobayashi under a different name. *Deltadiscus* has the same type species as *Eodiscus*, described under another name. *Eopagetia* and *Mesopagetia* do not seem to the writer sufficiently distinguishable from *Pagetia* to be valid subgenera. Finally, *Alemtejoia* is based on a species that R. and E. Richter consider identical with the type of *Delgadoia*.

Rasetti (1945) erected the genus *Pagetides* with the type *Pagetides elegans* Rasetti.

Westergård (1946) established the genus

[1] Dr. Stubblefield called the writer's attention to the fact that two of the generic names used by Lermontova are homonyms. *Cobboldia* was used by Brauer in 1887 for an insect and by Leiper in 1910 for a nematode. *Pagetina* was used by Barnard in 1931 for a crustacean.

It does not seem necessary, at least for the present, to replace *Pagetina*, as the forms assigned to that genus may be included in *Pagetia*, or more precisely in *Eopagetia* Kobayashi if that subgenus is recognized. However, *Cobboldia* seems to be zoologically valid and requires a new name. Impossibility of communicating with Dr. Lermontova in the present international situation does not enable the writer to follow the procedure, customary in similar cases, of calling the author's attention to the homonymy and suggesting that she propose a new name. Hence the writer ventures to suggest the new generic name *Neocobboldia* to replace *Cobboldia* Lermontova, 1940 (in Vologdin, Atlas of the leading forms of the fossil faunas of the USSR, p. 120), nec *Cobboldia* Brauer, 1887, nec *Cobboldia* Leiper, 1910.

Aulacodiscus for *Aulacodiscus bilobatus* Westergård. The preoccupied name *Aulacodiscus* was replaced by *Opsidiscus* Westergård, 1950.

Shaw (1950) affirmed that *Dipharus insperatus* Clark and *Ptychoparia attleborensis* Shaler and Foerste represent a larval form and the adult of the same species. Hence *Hebediscus* Whitehouse, 1936, becomes a synonym of *Dipharus* Clark, 1923.

A few remarks on the family names used for eodiscids are added. Raymond (1913) included the entire group in the family Eodiscidae, and the same procedure was followed by R. and E. Richter (1941). Resser (1937) proposed that the family name be changed to Dawsoniidae, for reasons that R. and E. Richter showed to be entirely unfounded, whether one accepts *Dawsonia* as available or not. Kobayashi (1935) erected the family Pagetiidae for the oculate forms, and this usage is followed in this paper. In 1943 Kobayashi distributed the eodiscids among five families, Eodiscidae, Dawsoniidae, Weymouthiidae, Pagetiidae and Hebediscidae.

CLASSIFICATION OF THE EODISCIDA

The Eodiscida are sharply separated from all other known trilobites (Rasetti, 1948a). Whether this fact is acknowledged by setting off these forms as an order or as a superfamily is of little importance.

Kobayashi (1944) suggests that certain Lower Cambrian forms bridge to some extent the gap between the agnostids and the eodiscids. A careful study of the forms in question does not substantiate Kobayashi's contention. On the contrary, all the material known to the writer confirms the sharp distinction between the agnostids and the eodiscids (Rasetti, 1948a).

As a basis for subdivision of the eodiscids, two characters readily lend themselves to taxonomic use because of their sharpness: the presence or lack of eyes and facial sutures, and the number of thoracic segments. Unfortunately the complete thorax is known only in a few species.

The writer agrees with the conclusion reached by R. and E. Richter that the sutureless forms are degenerate descendants of more primitive species with eyes and facial sutures; it is also likely that eyes and sutures were independently lost in several lines of descent. In view of the incomplete knowledge of the group, it seems expedient to divide the eodiscids into two families, the Pagetiidae including all the forms with eyes and facial sutures, and the Eodiscidae comprising all the sutureless forms, even though such groups may not represent phylogenetic units. The number of thoracic segments is used for generic distinction, species with two and three segments occurring among both the Pagetiidae and the Eodiscidae.

On the nomenclatural basis discussed in the preceding section, the North American eodiscids are classified as follows (each generic name is followed by the type species and the manner of designation).

Family EODISCIDAE Raymond, 1913
- EODISCUS Hartt in Walcott, 1884 (*Eodiscus pulchellus* Hartt in Walcott = *Microdiscus scanicus* Linnarsson, by monotypy).
- CALODISCUS Howell, 1935 (*Agnostus lobatus* Hall, by original designation).
- DAWSONIA Hartt in Dawson, 1868 (*Microdiscus dawsoni* Hartt in Dawson, by monotypy).
- WEYMOUTHIA Raymond, 1913 (*Agnostus? nobilis* Ford, by original designation).
- SERRODISCUS R. and E. Richter, 1941 (*Eodiscus* (*Serrodiscus*) *serratus* R. and E. Richter, by original designation).

Family PAGETIIDAE Kobayashi, 1935
- PAGETIA Walcott, 1916 (*Pagetia bootes* Walcott, by original designation).
- PAGETIDES Rasetti, 1945 (*Pagetides elegans* Rasetti, by original designation).
- DIPHARUS Clark, 1923 (*Dipharus insperatus* Clark = *Ptychoparia attleborensis* Shaler and Foerste, by original designation).

The present revision is confined to the North American forms of the family Eodiscidae.

Species previously described under the genus *Microdiscus* that do not belong to the family Eodiscidae are listed below.

Microdiscus connexus Walcott. The writer (Rasetti, 1948a) showed that this species possesses eyes and facial sutures and should be referred to *Pagetia*.

Microdiscus parkeri Walcott. Walcott figured a shield with unfurrowed axial and pleural lobes as a cephalon and a furrowed shield as a pygidium. His interpretation was not questioned by later authors who discussed the species. Examination of the type material revealed that it consists of nine poorly preserved internal casts, including: (a) one furrowed pygidium figured by Wal-

cott; (b) seven pygidia with unfurrowed axial and pleural lobes, one of which was figured by Walcott as a cephalon; (c) one very poor, unfigured cranidium with eyes and facial sutures, evidently representing a species of *Pagetides*. The pygidia include two species, and the cranidium probably belongs to one of them. The name *parkeri* is hereby restricted to the smooth pygidium, the lectotype being the specimen figured by Walcott (1886, pl. 16, fig. 2). This pygidium almost certainly belongs to a species of *Pagetides*, henceforth to be designated as *Pagetides parkeri*.

LOCATION OF TYPES

The North American material discussed in this paper is preserved at the institutions designated by the following abbreviations:

AMNH = American Museum of Natural History, New York, N. Y.
CU = Department of Geology, Cornell University, Ithaca, N. Y.
MCZ = Museum of Comparative Zoölogy at Harvard College, Cambridge, Mass.
NYSM = New York State Museum, Albany, N. Y.
ROM = Royal Ontario Museum of Palaeontology, Toronto, Ontario.
USNM = U. S. National Museum, Washington, D. C.

SYSTEMATIC DESCRIPTIONS

Family EODISCIDAE Raymond, 1913

Genus CALODISCUS Howell, 1935

Goniodiscus RAYMOND, 1913 [objective synonym, preoccupied].
Brevidiscus KOBAYASHI, 1943 [type: *Brevidiscus lunulatus* Kobayashi = *Calodiscus lobatus* (Hall)].

Description.—Cephalon semicircular. Glabella conical or cylindrical, with shallow transglabellar furrows or unfurrowed. Occipital furrow more or less distinct, occipital ring rounded or extended into a short spine. Cheeks convex, elevated posteriorly, sloping steeply to the marginal furrow. Marginal furrow expanded mesially into a preglabellar depression. Rim smooth or tuberculated.

Thorax unknown. Pygidium very convex; axis prominent, wide, almost reaching the marginal furrow, composed of about five segments. Pleural lobes furrowed or smooth; marginal furrow and rim narrow. The margin may be faintly serrated.

Type.—*Agnostus lobatus* Hall.

Stratigraphic and geographic range.—Lower Cambrian of the Northern Appalachians, Newfoundland and Shropshire, England.

Remarks.—*Calodiscus* is closely related to *Serrodiscus*, from which it is here separated on the basis of the much smaller size of all the known species, semicircular rather than semielliptical cephalon, and especially the small number of segments composing the pygidial axis. The presence of furrows on the pleural lobes is not considered of generic importance (R. and E. Richter, 1941), hence both species with furrowed and unfurrowed pleural lobes are included in *Calodiscus*.

Brevidiscus Kobayashi is based, according to the original designation, on "*Brevidiscus lunulatus* Kobayashi, nov. (= *Microdiscus lobatus* by Walcott, 1886, pl. 15, fig. 1a)." On the same page (Kobayashi, 1943a, p. 39) another new species, *Brevidiscus troyensis*, is stated to have as holotype the specimen indicated as "*Microdiscus lobatus* by Walcott, 1886, pl. 16, fig. 1a." The first indication of Walcott's plate (15 instead of 16) is an obvious error, as plate 15 has only one figure, representing *Protocaris marshi*. Hence both *lunulatus* and *troyensis* have the same specimen as holotype and are objective synonyms of each other. Furthermore, this specimen is perfectly typical of *Calodiscus lobatus* (see illustration in this paper, pl. 51, fig. 1), hence *Brevidiscus* is a synonym of *Calodiscus*.

In his extensive monograph of the eodiscids, Kobayashi (1944) contradicted his previous statement, affirming that the holotype of *Brevidiscus lunulatus* is a specimen from the Comley limestone of Shropshire designated as "*Microdiscus lobatus* by Lake, 1907, pl. 3, fig. 5." Examination of material from this locality supports Kobayashi's contention that the English specimens cannot be assigned to *lobatus;* but the name *lunulatus* cannot be applied to them, because this name was previously based on an American specimen of *lobatus*. It is here proposed that the British form be named *Calodiscus lakei*, the holotype being the specimen figured by Lake (1907, pl. 3, fig. 5). The main character that distinguishes

the new species from *lobatus* is the cylindrical rather than conical glabella.

CALODISCUS LOBATUS (Hall)
Plate 51, figures 1–11

Agnostus lobatus HALL, 1847, Palaeont. New York, vol. 1, p. 258, pl. 57, figs. 5a–f.
Microdiscus lobatus (Hall). FORD, 1858, Amer. Jour. Sci., ser. 3, vol. 6, p. 135.
Microdiscus lobatus (Hall). WALCOTT (part), 1886, U. S. Geol. Survey Bull. 30, p. 156, pl. 16, figs 1a–b (only).
Microdiscus lobatus (Hall). WALCOTT (part), 1890, U. S. Geol. Survey Tenth Ann. Rept., vol. 1, p. 632, pl. 81, figs. 4a–b (only).
Goniodiscus lobatus (Hall). RAYMOND, 1913, Ottawa Nat., vol. 27, p. 102, fig. 11.
Calodiscus lobatus (Hall). HOWELL, 1935, Jour. Paleontology, vol. 9, p. 224.
Brevidiscus lunulatus KOBAYASHI, 1943, Proc. Imp. Acad. Tokyo, vol. 19, p. 39.
Brevidiscus (?) troyensis KOBAYASHI, 1943, Proc. Imp. Acad. Tokyo, vol. 19, p. 39.
Brevidiscus (?) troyensis KOBAYASHI, 1944, Jour. Fac. Sci. Imp. Univ. Tokyo, sec. 2, vol. 7, pt. 1, p. 47, pl. 1, fig. 2 (erroneously indicated as fig. 3).

Available material.—Hall's types in the American Museum of Natural History, Walcott's material in the U. S. National Museum, and topotypes collected by the writer. Large numbers of cephala and pygidia excellently preserved in crystalline limestone are extant.

Description.—Cephalon nearly semicircular, about 1½ times wider than long, of moderate relief. Glabella subconical, rounded in front, slightly convex longitudinally, sloping down from the elevated occipital ring to the low anterior end. Dorsal furrow deep posteriorly, shallow in front. Glabellar furrows absent or indistinct; occipital furrow shallow and straight; occipital ring long, rounded, extending farther back than the cheeks. Cheeks not greatly elevated. Marginal furrow well defined posteriorly and laterally, broadening to a shallow, ill-defined depression occupying the space between the front of the glabella and the rim. Rim fairly wide, smooth, forming a sharp angle at the posterolateral margin in correspondence with the geniculation of the thorax.

Thorax unknown. Pygidium very convex, 1½ times wider than long. Axis convex, elevated, appreciably wider than the pleural lobes, moderately tapered, rounded posteriorly, almost reaching the marginal furrow; composed of five segments including the terminal section. Pleural lobes convex, strongly downsloping, almost vertical near the marginal furrow, showing four pairs of pleural furrows including the anterior marginal furrow, and faint interpleural grooves. Marginal furrow well impressed, rim of moderate width, serrated, showing three or four pairs of blunt spines.

Surface of test smooth or indistinctly granulated. Length of largest cranidium 2.2 mm., of pygidium 1.8 mm.

Remarks.—Individuals of this species, particularly the cephala, show a certain variability in the shape of the glabella, distinctness of glabellar furrows, depth of the preglabellar depression, elevation of the rim, and other features. However, as these variable features were observed in individuals from the same piece of rock and no clear-cut forms could be separated, this is obviously a case of intraspecific variability.

C. lobatus differs from other species assigned to the genus in the conical, unfurrowed glabella and furrowed pleural lobes of the pygidium.

Horizon and locality.—Lower Cambrian; Schodack formation. Type locality: conglomeratic and regularly bedded limestones in the eastern part of the city of Troy, New York (USNM locality 27). Also collected from many other localities in Rensselaer and Washington Counties, New York (see list in Walcott, 1912).

Types.—Syntypes: AMNH 210. Plesiotypes: USNM 15394; 116361.

CALODISCUS SCHUCHERTI (Matthew)
Plate 51, figures 22–27

Microdiscus schucherti MATTHEW, 1896, Trans. New York Acad. Sci., vol. 15, p. 238, pl. 17, figs. 4a–b.
Eodiscus schucherti (Matthew). RAYMOND, 1913, Ottawa Nat., vol. 27, p. 104, fig. 5.

Available material.—The writer examined casts of Matthew's types, and a few additional topotypes identified by Matthew and preserved in the U. S. National Museum. The material is fairly well preserved in limestone and consists of separate cephala and pygidia.

Description.—Matthew gave a good original description of the species.

Remarks.—This species was designated by Raymond as the type of *Eodiscus*. In the section on nomenclature this choice was shown to be improper, because the type of

the genus had been established by Walcott.

Microdiscus schucherti seems best placed in *Calodiscus* as it agrees with *lobatus* in all essential characters of the cephalon. The absence of pleural furrows is not considered of generic importance.

Horizon and locality.—Lower Cambrian; Schodack formation. Limestone on ridge in the eastern part of the city of Troy, New York.

Types.—Syntypes: ROM 138.

CALODISCUS MEEKI (Ford)
Plate 51, figures 19–21

Microdiscus meeki FORD, 1876, Amer. Jour. Sci., 3rd ser., vol. 11, p. 371.
Microdiscus meeki Ford. WALCOTT, 1886, U. S. Geol. Survey Bull. 30, p. 155, pl. 16, fig. 4.
Microdiscus meeki Ford. WALCOTT, 1890, U. S. Geol. Survey Tenth Ann. Rept., pt. 1, p. 632, pl. 81, fig. 3.
Eodiscus meeki (Ford). RAYMOND, 1913, Ottawa Nat., vol. 27, p. 103, fig. 9.
Paradiscus meeki (Ford). KOBAYASHI, 1944, Jour. Fac. Sci. Imp. Univ. Tokyo, sec. 2, vol. 7, pt. 1, p. 50, pl. 2, fig. 7.

Available material.—The holotype, a well-preserved cephalon in limestone.

Description.—Ford gave a good original description of the species.

Remarks.—In the absence of the pygidium it is somewhat uncertain whether this species should be referred to *Calodiscus* or *Serrodiscus*, but the cephalic features agree better with the former genus. The cephalon of *Calodiscus meeki* closely resembles that of *C. helena*, differing chiefly in the different distribution of the convexity of the glabella and cheeks.

Horizon and locality.—Lower Cambrian; Schodack formation. Conglomeratic limestone on ridge in the eastern part of the city of Troy, New York.

Types.—Holotype: NYSM 4587.

CALODISCUS AGNOSTOIDES (Kobayashi)
Plate 51, figures 12–16

Microdiscus lobatus (Hall). WALCOTT (part), 1886, U. S. Geol. Survey Bull. 30, p. 156, pl. 16, fig. 1 (only).
Microdiscus lobatus (Hall). WALCOTT (part), 1890, U. S. Geol. Survey Tenth Ann. Rept., pt. 1, p. 632, pl. 81, fig. 4 (only).
Brevidiscus (?) agnostoides KOBAYASHI, 1943, Proc. Imp. Acad. Tokyo, vol. 19, p. 39.
Brevidiscus (?) agnostoides KOBAYASHI, 1944, Jour. Fac. Sci. Imp. Univ. Tokyo, sec. 2, vol. 7, pt. 1, p. 58, pl. 1, fig. 3 (not fig. 2 as erroneously indicated in legend of plate).

Available material.—The holotype and another cephalon from the type locality, besides a few additional cephala from the same formation but different localities. All specimens are well preserved in crystalline limestone.

Description.—Cephalon alone known. Cephalon semicircular, of moderate relief as a whole. Glabella well defined by a deep dorsal furrow, subcylindrical, slightly expanded in the frontal lobe; flat longitudinally except for the steep slope to the marginal furrow. Two pairs of glabellar furrows impressed in the form of shallow, straight transglabellar furrows, dividing the glabella into three lobes of which the frontal one is somewhat longer than the other two. Occipital furrow deeper than the glabellar furrows; occipital ring about as long as the frontal glabellar lobe, rounded in the holotype and several other specimens, in others showing a small spine. Cheeks convex, most elevated in the median portion. Marginal furrow and rim as in *Calodiscus lobatus*. Surface of test finely granulated. Length of holotype cephalon 1.2 mm., width 1.5 mm.

Remarks.—Owing to the small size of the specimens, the question arises whether this might not be an immature form of one of the associated species, *Calodiscus lobatus* and *C. meeki*. We may immediately exclude that *agnostoides* is an immature form of *lobatus* because cephala of the latter species 1 mm. long already show the features of the adult. It is not certain that *agnostoides* is not based on a young cephalon of *Calodiscus meeki*. The cephala of the type and other specimens of *agnostoides* are 1–1.2 mm. long, while the only known cephalon of *meeki* has a length of 2.8 mm. Stages of growth might explain the differences, which are essentially the slight expansion of the frontal lobe of the glabella and the lack of marginal tubercles in *agnostoides*. Awaiting the discovery of additional material, *agnostoides* is provisionally recognized as distinct. The above-mentioned character of the glabella also distinguishes the present species from the others assigned to the genus.

Horizon and locality.—Lower Cambrian; Schodack formation. Type locality USNM 27, conglomeratic limestone in the eastern suburb of the city of Troy, New York. Other localities: USNM 33, roadside near Rock Hill schoolhouse, near North Green-

wich; USNM 33b, M. C. Tefft's farm, 1.5 miles ESE of North Greenwich; USNM 34, roadside W of bridge on Poultney River at Low Hampton; and USNM 36a, 3 miles NE of North Greenwich; all in Washington County, New York.

Types.—Holotype: USNM 116356. Plesiotypes: USNM 116357–9.

CALODISCUS cf. C. AGNOSTOIDES (Kobayashi)

Plate 51, figures 17, 18

Available material.—A single cephalon preserved in limestone.

Description.—Cephalon similar to that of *C. agnostoides*, differing in the larger size, greater proportional length and stronger elevation of the frontal glabellar lobe, and presence of a well-developed occipital spine. Length 2.8 mm. Surface smooth.

Remarks.—Since the only known cephalon is considerably larger than the typical cephala of *C. agnostoides*, there is the possibility that this may be the full-grown form of that species. The question can be settled only by the discovery of additional material.

Horizon and locality.—Lower Cambrian; Schodack formation. Locality USNM 43a, one mile ENE of Salem, Washington County, New York.

Figured specimen.—USNM 116360.

CALODISCUS HELENA (Walcott)

Plate 54, figures 18–22

Microdiscus helena WALCOTT, 1889, Proc. U. S. Nat. Mus., vol. 12, p. 40.
Microdiscus helena WALCOTT, 1890, U. S. Geol. Survey Tenth Ann. Rept., pt. 1, p. 632, pl. 81, figs. 1, 1a.
Eodiscus helena (Walcott). RAYMOND, 1913, Ottawa Nat., vol. 27, p. 103, fig. 6.
Paradiscus helena (Walcott). KOBAYASHI, 1943, Proc. Imp. Acad. Tokyo, vol. 19, p. 38.
Paradiscus helena (Walcott). KOBAYASHI, 1944, Jour. Fac. Sci. Imp. Univ. Tokyo, sec. 2, vol. 7, pt. 1, p. 44, pl. 2, figs. 1a–b.

Available material.—Walcott's type lot consists of two cephala and five pygidia preserved as internal casts in soft, dark-brown, earthy residue from leached impure limestone.

Description.—Walcott's orginal description is adequate.

Remarks.—The cephalon of this species resembles that of *C. meeki*, differing chiefly in the proportions of the glabellar lobes and strong elevation of the posterior portions of the glabella and cheeks. The pygidium agrees with *Calodiscus* in the small number of axial segments but has unfurrowed pleural lobes like *Serrodiscus*. In agreement with the principle that the number of segments present is more important than the distinctness of their appearance (R. and E. Richter, 1941), the writer believes that the pygidium favors reference of the species to *Calodiscus*.

Horizon and locality.—Lower Cambrian. Locality USNM 41; decomposed limestone 600 meters west of Manuel's Brook, Conception Bay, Newfoundland. Associated with *Dipharus attleborensis*, *Strenuella* sp., *Serrodiscus bellimarginatus*.

Types.—Syntypes: USNM 18361.

CALODISCUS WALCOTTI Rasetti, n. sp.

Plate 54, figure 17

Available material.—Known from a single cephalon preserved in limestone.

Description.—Cephalon of moderate convexity. Glabella on the average tapered, especially in the frontal lobe that is sharply pointed; defined by a deep dorsal furrow. Two pairs of glabellar furrows impressed all across the glabella, deeper laterally. Occipital furrow impressed at the sides; occipital ring and posterior glabellar lobe apparently extended together into a strong spine, broken off in the available specimen. Cheeks of considerable convexity, sloping down steeply to the marginal furrow. Rim well defined, convex, of even width except for the frontal portion which expands backward, thus causing the marginal furrow to coalesce with the dorsal furrow. Surface of test granulated. Length of cephalon 2.9 mm., width 3.5 mm.

Remarks.—This form, although represented by a single individual, was deemed worth describing because it does not closely resemble any previously known species. The chief difference from other species of *Calodiscus* is the lack of a broad preglabellar depression. In the proportions and convexity of the various cephalic parts, *Calodiscus walcotti* remarkably resembles *Pagetides elegans* Rasetti, except for the total absence of eyes and facial sutures.

Horizon and locality.—Lower Cambrian; Schodack formation. Locality USNM 36b, near Schoolhouse no. 12, near Greenwich, Washington County, New York.

Types.—Holotype: USNM 26710.

Genus SERRODISCUS R. and E. Richter, 1941

Paradiscus KOBAYASHI, 1943 [type: *Microdiscus speciosus* Ford].

Description.—R. and E. Richter characterized *Serrodiscus* as follows: "A subgenus which is distinguished from *Eodiscus* (*Eodiscus*) with the type *E.* (*E.*) *schucherti* Matthew by the following characteristics of the tail. Tail long. Axis long with very many (at least 8+ to 14+) rings; wider than a pleural lobe. The rim has a tendency to form denticulations, mostly directed downward."

The generic description may be supplemented as follows. Cephalon semiellipticaI. Glabella long, tapered, with shallow furrows or unfurrowed. Occipital ring simple or bearing a small spine. Fixed cheeks separated by a short preglabellar depression. Rim of even width, bearing a few large tubercles. Thorax of three segments, possessing the faculty of enrollment. Pygidium considerably more convex than the cephalon, subtriangular. Surface of test not conspicuously ornamented. Size large for an eodiscid, adult shields reaching lengths of 20–30 mm.

Type.—Eodiscus (*Serrodiscus*) *serratus* R. and E. Richter.

Stratigraphic and geographic range.—Lower Cambrian of the Acado-Baltic and Appalachian provinces.

Remarks.—The genus comprises a small, homogeneous group of species from the Lower Cambrian of the Acado-Baltic province of Europe (*serratus* R. and E. Richter, *silesius* R. and E. Richter), the Acado-Baltic province of North America (*bellimarginatus* Shaler and Foerste) and the northern Appalachian province (*speciosus* Ford). A doubtfully distinct species is *Paradiscus robustus* Kobayashi, based on English specimens identified as *speciosus* by Lake.

Serrodiscus is closely related to *Calodiscus*, from which it differs chiefly in the semielliptical cephalon, large number of segments composing the pygidial axis, and large size of the shield.

SERRODISCUS SPECIOSUS (Ford)
Plate 52, figures 1–11

Microdiscus speciosus FORD, 1873, Amer. Jour. Sci., 3rd ser., vol. 6, p. 137, figs. 2 a–b. 1877, ibid., 3rd ser., vol. 13, p. 141.

Microdiscus speciosus Ford. WALCOTT, 1886, U. S. Geol. Survey Bull. 30, p. 154, pl. 16, figs. 3, 3a–c.

Microdiscus speciosus Ford. WALCOTT, 1890, U. S. Geol. Survey Tenth Ann. Rept., pt. 1, p. 632, pl. 81, figs. 5, 5a–c.

Microdiscus speciosus Ford. MATTHEW, 1896, Trans. New York Acad. Sci., vol. 15, p. 236, pl. 17, fig. 6.

Eodiscus speciosus (Ford). RAYMOND, 1913, Ottawa Nat., vol. 27, p. 102, fig. 3.

Eodiscus (*Serrodiscus*) *speciosus* (Ford). R. & E. RICHTER, 1941, Abh. senckenberg. naturf. Ges., no. 455, p. 27, pl. 1, figs. 15–21; pl. 4, fig. 61.

Paradiscus speciosus (Ford). KOBAYASHI, 1943, Proc. Imp. Acad. Tokyo, vol. 19, p. 38.

Paradiscus speciosus (Ford). KOBAYASHI, 1944, Jour. Fac. Sci. Imp. Univ. Tokyo, sec. 2, vol. 7, pt. 1, p. 50, pl. 1, fig. 4.

Available material.—The writer examined Ford's original types and additional specimens collected by the same author; plesiotypes described and figured by Walcott; and specimens collected by the writer at the type locality and elsewhere.

EXPLANATION OF PLATE 53

FIGS. *1–6—Eodiscus punctatus* (Salter). *1*, Surface of shale with numerous cephala and pygidia, ×4; USNM 26700, plesiotype. *2*, *5*, Cephala, ×8; USNM 26700, plesiotypes. *3*, *4*, Pygidia, ×8; USNM 26700, plesiotypes. *6*, Entire shield, ×8; USNM 26315, plesiotype. All figures represent artificial rubber casts of natural external impressions and show the ornamentation of the external surface. Locality USNM 225m–o; shale of the *Paradoxides davidis* zone at Manuels Brook, Conception Bay, Newfoundland. (p. 448)

7–16—Eodiscus scanicus (Linnarsson). *7*, *10*, *16*, Artificial casts from external impressions of cephala in various stages of growth, ×8. *8*, Artificial cast of cephalon showing appearance of internal surface, ×8. *9*, Dorsolateral view of artificial cast from external impression of cephalon, ×8. *11–13*, Artificial casts of external impressions of pygidia in various stages of growth, ×8. *14*, *15*, Artificial casts of external impressions of very young pygidia, showing pleural furrows on external surface, ×12. USNM 116353, plesiotypes. Collected by the author from shale of the Porter Road formation at Hanford Brook, New Brunswick. See also plate 54, figs. *10–16*. (p. 447)

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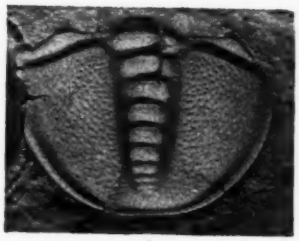
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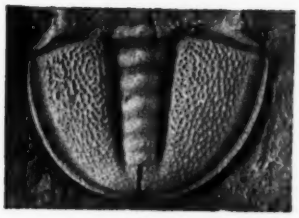
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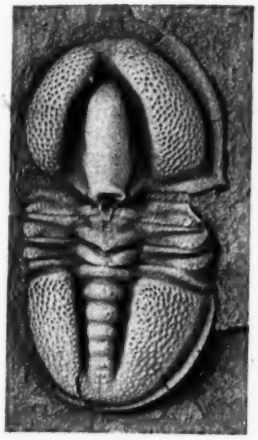
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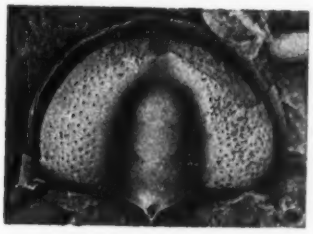
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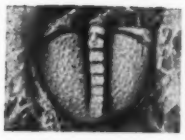
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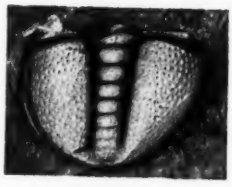
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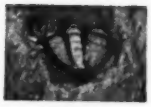
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Rasetti, eodiscid trilobites

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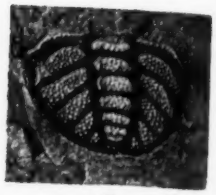
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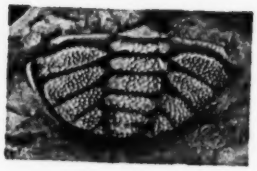
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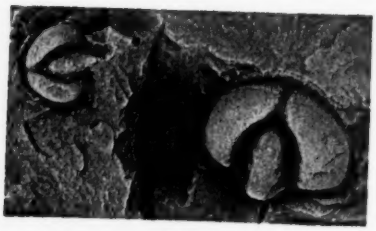
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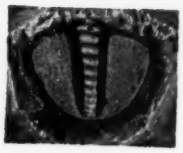
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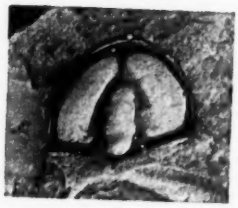
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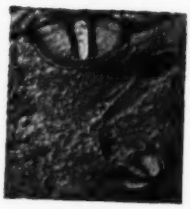
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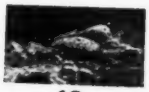
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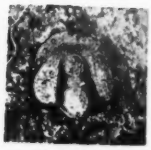
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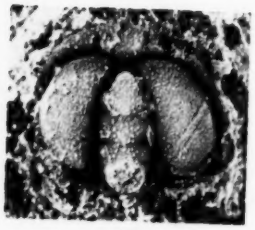
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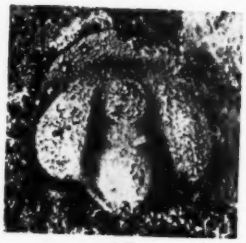
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Rasetti, eodiscid trilobites

All specimens are from fairly to excellently preserved in dark-gray, finely crystalline limestone and generally show little or no flattening or distortion. A few articulated shields are extant.

Description.—Ford gave a good description of the species. However, two features apparently escaped the attention of all the authors who studied this form. The pygidial rim possesses a row of small, downward-directed spines, about ten in number on each side. Unless the specimen is appropriately prepared these spines cannot be observed. Another feature is the presence of exceedingly short and slender genal spines, either concealed by the matrix or broken off in most of the available specimens. The variability in the number of tubercles on the cephalic rim has already been noticed by previous authors.

Remarks.—The presence of marginal pygidial spines brings the species still closer to the type of the genus and makes entirely unnecessary a separate genus *Paradiscus*.

Horizon and locality.—Lower Cambrian; Schodack formation. Type locality is the ridge in the eastern suburb of the city of Troy, New York. Also collected by Ford and Walcott at numerous other localities in Rensselaer and Washington Counties, New York (see list in Walcott, 1912). The species was also reported by Walcott from the conglomerates at Bic, Quebec, but the writer has been unable to locate the specimens. For the localities outside North America, see R. and E. Richter (1941).

Types.—Lectotype: NYSM 4588. Paratype: NYSM 4589. Plesiotype collected by Ford and figured by Walcott: NYSM 4590. Plesiotypes figured by Walcott and the writer: USNM 17478. Other specimens: USNM 15398

SERRODISCUS BELLIMARGINATUS
(Shaler and Foerste)
Plate 52, figures 12–17

Microdiscus belli-marginatus SHALER & FOERSTE, 1888, Bull. Harvard Mus. Comp. Zoöl., vol. 16, no. 2, p. 35, pl. 2, figs. 19, 19a.

Microdiscus bellimarginatus Shaler & Foerste. WALCOTT, 1890, U. S. Geol. Survey Tenth Ann. Rept., pt. 1, p. 630, pl. 18, figs. 2a, 2a–b.

Microdiscus bellicinctus Shaler & Foerste. MATTHEW, 1896, Trans. New York Acad. Sci., vol. 15, p. 237.

Microdiscus bellimarginatus mut. *insularis* MATTHEW, 1899, Trans. Royal Soc. Canada, 2nd ser., vol. 5, sec. 4, p. 75.

Eodiscus belli-marginatus (Shaler & Foerste). RAYMOND, 1913, Ottawa Nat., vol. 23, p. 103, fig. 7.

EXPLANATION OF PLATE 54

FIGS. *1–9*—*Dawsonia dawsoni* (Hartt in Dawson). *1*, Artificial cast of external impression of cephalon, ×8; USNM 116354, plesiotype. From shale of the *Paradoxides eteminicus* zone at Seely Street, St. John, New Brunswick. *2*, *3*, Cephala (internal casts), ×8. *4*, Cephalon (artificial cast from external impression), ×8. *5*, Pygidium (internal cast), ×8. *6*, *7*, Pygidia (artificial casts from external impressions), ×8. USNM 116355, plesiotypes. From shale of the Fossil Brook formation (*Paradoxides eteminicus* zone) at Fossil Brook, New Brunswick. *8*, Entire shield (internal cast), ×8; PU 73549, plesiotype. Horizon and locality same as fig. *1*. *9*, Entire shield (artificial cast from external impression), ×8; ROM 556, plesiotype. Horizon and locality same as fig. *1*. (p. 449)

10–16—*Eodiscus scanicus* (Linnarsson). *10*, Cephala (internal casts), ×5. *11*, Pygidium (internal cast), ×5; CU 3794, syntypes of *Eodiscus pulchellus*. From shale of the Porter Road formation, St. John, New Brunswick. *12*, Cephalon (internal cast), ×5. *13*, *14*, Pygidia (internal casts), ×5; ROM 558, Matthew's plesiotypes of *Microdiscus pulchellus*. From shale of the Porter Road formation at Porter Road, New Brunswick. *15*, Cephalon (internal cast), ×8; ROM 47, holotype of *Microdiscus precursor*. From shale of the Porter Road (?) formation at Hanford Brook, New Brunswick. *16*, Pygidium and cephalon (internal casts, longitudinally compressed, ×12); ROM 47, pygidium of Matthew's *Microdiscus precursor*, Kobayashi's holotype of *Dawsonia canadensis*. Horizon and locality same as preceding. (p. 447)

17—*Calodiscus walcotti* Rasetti, n. sp. Cephalon, ×8; USNM 26710, holotype. From limestone of the Schodack formation at USNM locality 36b; near Greenwich, Washington County, New York. (p. 443)

18–22—*Calodiscus helena* (Walcott). *18*, Cephalon, ×10. *19*, *20*, Lateral and dorsal views of the same cephalon, ×5. *21*, *22*, Pygidia, ×5. USNM 18361, syntypes. All the specimens are internal casts and were collected from USNM locality 41: limestone 600 meters west of Manuels Brook, Conception Bay, Newfoundland. (p. 443)

Eodiscus (*Serrodiscus*) *bellimarginatus* (Shaler & Foerste). R. & E. RICHTER, 1941, Abh. senckenberg. naturf. Ges., no. 455, p. 23.
Eodiscus (*Serrodiscus*) *insularis* (Matthew). R. & E. RICHTER, 1941, Abh. senckenberg. naturf. Ges., no. 455, p. 23.
Eodiscus bellimarginatus (Shaler & Foerste). KOBAYASHI, 1944, Jour. Fac. Sci. Imp. Univ. Tokyo, sec. 2, vol. 7, pt. 1, p. 52, pl. 1, figs. 5a–b.
Eodiscus (*Serrodiscus*) *bellimarginatus* (Shaler & Foerste). SHAW, 1950, Jour. Paleontology, vol. 24, p. 582, pl. 79, figs. 19–23.

Available material.—The writer examined the specimens, in part possibly syntypes, preserved in the Museum of Comparative Zoölogy. Casts of the types of *Microdiscus bellimarginatus insularis* and material from Newfoundland studied by Walcott were available.

All the specimens are preserved as internal and external casts in dark-brown, earthy residue from leached impure limestone.

Description.—The species was recently described by Shaw on the basis of topotype material.

Remarks.—Matthew separated the form *insularis* stating that it differs from the types of the species in having a narrower head and pygidium and fewer tubercles on the rim. He also affirmed that the specimens from Newfoundland described and figured by Walcott are intermediate between *bellimarginatus* and *insularis*. As far as the material allows an accurate comparison, no specific differences can be detected between the specimens from Massachusetts and those from Newfoundland studied by Walcott and Matthew. The proportions of the shields are the same, and the number of tubercles on the cephalic rim, even if it should present differences, is hardly of specific value, witness the great variability in this character shown by *Serrodiscus speciosus*. Hence *insularis* is placed in synonymy with *bellimarginatus*.

The present species differs from *speciosus* chiefly in the less tapered glabella, presence of an occipital spine, more conspicuous genal spines, nodes on the axial rings, and stronger marginal spines.

Horizon and locality.—Lower Cambrian. Type formation and locality: Hoppin limestone, Hoppin Hill, near North Attleboro, Massachusetts. Also collected by Walcott and Matthew at Manuels, Conception Bay, Newfoundland (USNM locality 41). Associated with *Strenuella strenua*, *Calodiscus helena*, *Dipharus attleborensis*.

Types.—The location of the types of *Microdiscus bellimarginatus* and the other trilobites described by Shaler and Foerste is doubtful. Twenty-one specimens preserved in the Museum of Comparative Zoölogy are the only topotypes known to the writer; one of these (MCZ 4811) was stated by Shaw to represent a paratype. Syntypes of *Microdiscus bellimarginatus insularis:* ROM 145, 750. Plesiotypes from Newfoundland: USNM 18329.

Genus WEYMOUTHIA Raymond, 1913

Delgadoia VOGDES, 1917 [type: *Microdiscus caudatus* Delgado].
Delgadodiscus KOBAYASHI, 1935 [type: *Microdiscus caudatus* Delgado].
Alemtejoia KOBAYASHI, 1943 [type: *Microdiscus souzai* Delgado = *M. caudatus* Delgado].

Description.—Eodiscidae with dorsal furrows entirely or almost obsolete on cephalon and pygidium, lacking glabellar, axial and pleural furrows. Marginal furrow and rim distinct in both shields. Thorax of three segments.

Type.—*Agnostus ? nobilis* Ford.

Stratigraphic and geographic range.—Lower Cambrian of the Appalachian and Acado-Baltic provinces.

WEYMOUTHIA NOBILIS (Ford)
Plate 52, figure 18

Agnostus ? nobilis FORD, 1872, Amer. Jour. Sci., 3rd ser., vol. 3, p. 421, figs. 1, 2.
Agnostus nobilis Ford. WALCOTT, 1886, U. S. Geol. Survey Bull. 30, p. 150, pl. 16, fig. 7.
Agnostus nobilis Ford. WALCOTT, 1890, U. S. Geol. Survey Tenth Ann. Rept., pt. 1, p. 629, pl. 80, fig. 5.
Microdiscus ? nobilis (Ford). WALCOTT, 1890, U. S. Geol. Survey Tenth Ann. Rept., pt. 1, p. 629.
Weymouthia nobilis (Ford). RAYMOND, 1913, Ottawa Nat., vol. 27, p. 102, fig. 15, 16.
Weymouthia nobilis (Ford). RAYMOND, 1920, Connecticut Acad. Arts Sci., Mem. 7, p. 139, fig. 35.
Weymouthia nobilis (Ford). SHIMER & SHROCK, 1944, Index Fossils of North Amer., p. 619, pl. 252, fig. 16.
Weymouthia nobilis (Ford). KOBAYASHI, 1943, Proc. Imp. Acad. Tokyo, vol. 19, p. 40.
Weymouthia nobilis (Ford). KOBAYASHI, 1944, Jour. Fac. Sci. Imp. Univ. Tokyo, sec. 2, vol. 7, pt. 1, p. 67, pl. 1, fig. 16.
Weymouthia nobilis (Ford). SHAW, 1950, Jour. Paleontology, vol. 24, p. 584, pl. 79, fig. 24.

Available material.—One specimen from Weymouth, Massachusetts tentatively assumed to represent the species.

Description.—Ford's original description is the only one based on material representing the species with certainty.

Remarks.—Shaw (1950) gave a discussion of the status of this species. The holotype was already reported lost in 1890 and no specimens from the type formation are extant. The only North American specimen known to the writer was collected from another formation in a different sedimentary province. The species was also reported from England and Norway, but as pointed out by Shaw (1950) the identification of these specimens is also doubtful.

Horizon and locality.—Lower Cambrian; Schodack formation. Ridge in the eastern part of the city of Troy, New York. The specimen tentatively assigned to the species was collected from the Weymouth formation at Weymouth, Massachusetts.

Types.—The holotype is lost. Plesiotype: MCZ 246.

Genus EODISCUS Hartt in Walcott, 1884

Microdiscus SALTER, 1864; Walcott, 1884; Matthew, 1896 (not Emmons, 1855) [type: *Microdiscus punctatus* Salter].

Spinodiscus KOBAYASHI, 1943 [type: *Microdiscus punctatus* Salter].

Deltadiscus KOBAYASHI, 1943 [type: *Microdiscus punctatus precursor* Matthew = *Microdiscus scanicus* Linnarsson].

Description.—Glabella tapered, elevated posteriorly, defined by a deep dorsal furrow. Glabellar and occipital furrows impressed at the sides; occipital ring extended into a strong spine. Cheeks separated in front by a deep median preglabellar furrow. Cephalic rim uniformly narrow, flat, with fine crenulations visible only on the internal surface. Thorax of three segments; ends of pleura of first segment pointing backward, of third segment pointing forward. Pygidium with long, narrow axis defined by a deep dorsal furrow; axis furrowed for entire length, composed of ten or more segments. Pleural lobes unfurrowed in adult; pygidial rim narrow. Surface punctate or tuberculated.

Type.—*Eodiscus pulchellus* Hartt in Walcott = *Microdiscus scanicus* Linnarsson.

Stratigraphic and geographic range.—Middle Cambrian of the Acado-Baltic province.

Remarks.—*Eodiscus* differs from *Calodiscus* in the presence of a well-defined preglabellar furrow, narrow and depressed cephalic rim, strong occipital spine, and large number of segments in the pygidial axis. The first three characters and the narrow pygidial axis distinguish it from *Serrodiscus*, in addition to the lack of marginal pygidial spines. *Eodiscus* differs from *Dawsonia* in the lack of coarse crenulations on the cephalic rim, presence of a sharp preglabellar furrow, number of thoracic segments, narrower and longer pygidium with unfurrowed pleural lobes.

The author of the genus and the designation of the genotype were already discussed.

EODISCUS SCANICUS (Linnarsson)
Plate 53, figures 7–16; plate 54, figures 10–16

Microdiscus scanicus LINNARSSON, 1883, Sveriges Geol. Unders., ser. C, no. 54, p. 29, pl. 4, figs. 17, 18.

Microdiscus punctatus Salter (part). WALCOTT, 1884, U. S. Geol. Survey Bull. 10, p. 24, pl. 2, figs. 1, 1a–c.

Eodiscus pulchellus Hartt in WALCOTT, 1884, U. S. Geol. Survey Bull. 10, p. 24.

Microdiscus punctatus var. *pulchellus* Hartt. MATTHEW, 1886, Trans. Roy. Soc. Canada, vol. 3, sec. 4, p. 74, pl. 7, figs. 12a–c.

Microdiscus punctatus var. *precursor* MATTHEW, 1886, Trans. Roy. Soc. Canada, vol. 3, sec. 4, p. 75, pl. 7, fig. 13.

Microdiscus precursor MATTHEW, 1896, Trans. New York Acad. Sci., vol. 15, p. 239, pl. 17, fig. 7, text fig.

Microdiscus pulchellus Hartt. MATTHEW, 1896, Trans. New York Acad. Sci., vol. 15, p. 242, pl. 17, figs. 8a–f.

Microdiscus punctatus Salter. LAKE (part), 1907, Palaeontogr. Soc., British Cambrian Trilob., p. 36, pl. 3, figs. 11–17.

Eodiscus pulchellus (Walcott). RAYMOND, 1913, Ottawa Nat., vol. 27, p. 103, fig. 2.

Eodiscus scanicus (Linnarsson). RAYMOND, 1913, Ottawa Nat., vol. 27, p. 104, fig. 10.

Eodiscus praecursor (Matthew). RAYMOND, 1913, Ottawa Nat., vol. 27, p. 103, fig. 8.

Spinodiscus punctatus scanicus (Linnarsson). KOBAYASHI, 1943, Proc. Imp. Acad. Tokyo, vol. 19, p. 39.

Spinodiscus matthewi KOBAYASHI, 1943, Proc Imp. Acad. Tokyo, vol. 19, p. 39.

Deltadiscus praecursor (Matthew). KOBAYASHI, 1943, Proc. Imp. Acad. Tokyo, vol. 19, p. 39.

Deltacandus praecursor (Matthew) [error for *Deltadiscus*]. KOBAYASHI, 1943, Proc. Imp. Acad. Tokyo, vol. 19, p. 39.

Deltadiscus praecursor (Matthew). KOBAYASHI, 1944, Jour. Fac. Sci. Imp. Univ. Tokyo, sec. 2, vol. 7, pt. 1, p. 60, pl. 1, fig. 10.

Dawsonia canadensis KOBAYASHI, 1944, Jour.

Fac. Sci. Imp. Univ. Tokyo, sec. 2, vol. 7, pt. 1, p. 60, pl. 2, fig. 14.

Eodiscus pulchellus (Hartt). KOBAYASHI, 1944, Jour. Fac. Sci. Imp. Univ. Tokyo, sec. 2, vol. 7, pt. 1, p. 52.

Eodiscus punctatus scanicus (Linnarsson). WESTERGÅRD, 1946, Sveriges Geol. Unders., ser. C, no. 477, p. 25, pl. 1, figs. 6–11.

Available material.—Specimens from New Brunswick labeled by Hartt *Eodiscus pulchellus* and studied by Walcott in 1884; casts of the specimens on which Matthew based his description of the species in 1886 and 1896 under the names *Microdiscus pulchellus* and *Microdiscus precursor;* abundant material from New Brunswick in the U. S. National Museum and the writer's own collections; and topotypes from Sweden preserved in the U. S. National Museum.

All the material of this species known to the writer is preserved in fine-grained, black, siliceous shale, often without appreciable flattening or distortion. Although the test is seldom preserved, internal and external impressions give perfect reproductions of the ornamentation of both surfaces.

Description.—As the species was well described and illustrated by several of the authors cited in the references, particularly Matthew, Lake, Illing and Westergård, a description is not repeated.

Remarks.—Illing and Westergård agree that *E. eucentrus* is a synonym of *Eodiscus punctatus* and *E. pulchellus* of *E. scanicus*. They both consider *E. scanicus* a subspecies of *E. punctatus*, in view of the existence of intermediate forms. *E. punctatus* is younger than *E. scanicus* and probably descended from it. The writer, without in the least questioning Illing's and Westergård's observations, considers *E. scanicus* a separate species, because this form, under the name *Eodiscus pulchellus*, is the type of *Eodiscus*, and it appears preferable that it be acknowledged as a full-fledged species.

The specimens described and figured by Matthew (pl. 54, figs. 12–14) which Kobayashi designated as the types of a new species, *Spinodicus matthewi*, are typical of *Eodiscus scaniscus*. So is the cephalon (pl. 54, fig. 15) on which Matthew based *Microdiscus precursor*, designated by Kobayashi as the type of *Deltadiscus*. The pygidium (pl. 54, fig. 16) tentatively assigned by Matthew to *Microdiscus precursor* is a longitudinally compressed pygidium of *E. scanicus* in an early stage of development, as unquestionably shown by complete growth series collected by the writer; this pygidium is Kobayashi's type of *Dawsonia canadensis*. The writer's material here illustrated (pl. 53, figs. 7–16) is from the type locality for *Microdiscus precursor*.

Horizon and locality.—Type horizon and locality: Middle Cambrian (zone of *Tomagnostus fissus* and *Triplagnostus atavus*); Andrarum, Sweden. In North America, the species was collected only from the Porter Road formation (*Paradoxides abenacus* zone) at St. John (type locality for *Eodiscus pulchellus*), Porter Road, Hanford Brook (type locality for *Microdiscus precursor*), and other localities in New Brunswick (Hayes and Howell, 1937). Matthew's reference of this species, under the name *Microdiscus precursor*, to the *Paradoxides eteminicus* zone at Hanford Brook is probably erroneous.

Types.—Syntypes: State Museum for Natural History, Stockholm, Sweden. Types of *Eodiscus pulchellus*: CU 3794. Types of *Microdiscus precursor*: ROM 47. Plesiotypes of *Microdiscus pulchellus* described and figured by Matthew, designated by Kobayashi as syntypes of *Spinodiscus matthewi:* ROM 558. Plesiotypes of *Eodiscus pulchellus* probably collected by Hartt: USNM 14671. Plesiotypes collected and figured by the writer: USNM 116353.

EODISCUS PUNCTATUS (Salter)
Plate 53, figures 1–6

Microdiscus punctatus SALTER, 1864, Quart. Jour. Geol. Soc. London, vol. 20, p. 237, pl. 13, figs. 11a–c.

Microdiscus eucentrus LINNARSSON, 1883, Sveriges Geol. Unders., ser. C, no. 54, p. 30, pl. 4, figs. 19, 20.

Microdiscus (Eodiscus) punctatus Salter. MATTHEW, 1896, Trans. New York Acad. Sci., vol. 15, p. 244.

Microdiscus scanicus f. *eucentra* Linnarsson. GRÖNWALL, 1902, Dansk Geol. Unders., II Raekke, no. 13, p. 79, pl. 1, fig. 20.

Microdiscus punctatus Salter. LAKE (part), 1907, Palaeontogr. Soc., British Cambrian Trilob., p. 36, pl. 3, figs. 11, 12 (only).

Eodiscus punctatus (Salter). RAYMOND, 1913, Ottawa Nat., vol. 27, p. 103, fig. 1.

Microdiscus punctatus Salter. ILLING, 1916, Quart. Jour. Geol. Soc. London, vol. 71, p. 423, pl. 33, figs. 9, 10.

Spinodiscus punctatus (Salter). KOBAYASHI,

1943, Proc. Imp. Acad. Tokyo, vol. 19, p. 39.
Spinodiscus punctatus (Salter). KOBAYASHI, 1944, Jour. Fac. Sci. Imp. Univ. Tokyo, sec. 2, vol. 7, pt. 1, p. 55, pl. 1, fig. 7.
Eodiscus punctatus (Salter). WESTERGÅRD, 1946, Sveriges Geol. Unders., ser. C, no. 477, p. 24, pl. 1, figs. 12–15.

Available material.—Topotypes from Wales, specimens from Sweden, and abundant material from Newfoundland, all preserved in the U. S. National Museum.

All the examined specimens are preserved in fine-grained, black, siliceous shale and the test is usually absent. However, perfect impressions enable one to study the character of both surfaces. Part of the material is not appreciably flattened. Several entire shields are known.

Description.—As the species was well described by Matthew, Lake, Illing, Westergård and others, a description is not repeated.

Remarks.—*Eodiscus punctatus* differs from *E. scanicus* chiefly in the somewhat wider cephalic rim, greater length and horizontal direction of the occipital spine, and the change of the external surface of the pygidium from tuberculate to punctate taking place in later ontogenetic stages. A pygidium of *E. punctatus* 2 mm. long is already definitely punctate, while on a pygidium of *E. scanicus* of the same size, puncta and tubercles are about equally conspicuous.

Horizon and locality.—Type horizon and locality: Middle Cambrian (Menevian; *Paradoxides davidis* zone); Porth-y-rhaw, near St. David's, Wales. In North America, the species was apparently collected only from the *Paradoxides davidis* zone at Manuels, Newfoundland.

Types.—Syntypes: Sedgwick Museum, Cambridge, England. Plesiotypes from Manuels, Conception Bay, Newfoundland: USNM 25760, 26315, 26700.

Genus DAWSONIA Hartt in Dawson, 1868

Description.—Glabella tapered, indistinctly furrowed; occipital ring extended into a long spine. Cheeks elevated, separated in front by a short preglabellar depression. Cephalic rim elevated, fairly thick, with coarse crenulations. Thorax of two segments; ends of pleura of first segment pointing backward, of second segment pointing forward. Pygidium much wider than long, with long axis composed of six to seven segments, furrowed for its entire length; pleural lobes deeply furrowed. Surface strongly granulated in the type species.

Type.—*Microdiscus dawsoni* Hartt in Dawson.

Stratigraphic and geographic range.—Middle Cambrian of the Acado-Baltic province.

Remarks.—The genus deserves recognition because the type species is the only blind eodiscid definitely known to possess a thorax of two segments. This character differentiates *Dawsonia dawsoni* from *Eodiscus*, besides the proportionately longer glabella, broad preglabellar depression in place of a sharp longitudinal furrow, coarse crenulations of the cephalic rim, smaller number of segments in the pygidial axis, and deeply furrowed pleural lobes.

It is difficult, however, to determine the generic position of several forms that partake of the characters of *Eodiscus* and *Dawsonia*. On the basis of the cephalic and pygidial features, one should assign to *Dawsonia* also *Microdiscus sculptus* Hicks and *Calodiscus oelandicus* Westergård. However, Lake (1907) states that *Microdiscus sculptus* has probably three thoracic segments and possibly four. If this is true (the only known articulated shield is extremely poor) the species should be excluded from *Dawsonia* and either placed in *Eodiscus* or made the type of the genus *Metadiscus* Kobayashi. The number of segments in *Calodiscus oelandicus* is unknown. Two additional described forms, *Eodiscus borealis* Westergård and *Calodiscus foveolatus* Howell, have cephala like *Eodiscus* and pygidia like *Dawsonia*, while the thorax is unknown. Considering the cephalic characters as more important, a tentative reference of both species to *Eodiscus* seems indicated.

Several authors united *Dawsonia* with *Calodiscus*. In the writer's opinion, the two genera are not closely related. Both *Eodiscus* and *Dawsonia* probably derived from Lower or early Middle Cambrian species of *Pagetia*, while *Calodiscus* belongs to a stock that had lost eyes and facial sutures at a much earlier time.

DAWSONIA DAWSONI (Hartt in Dawson)
Plate 54, figures 1–9

Microdiscus dawsoni Hartt in DAWSON, 1868, Acadian Geol., 2nd ed., p. 654, fig. 228.

Microdiscus dawsoni Hartt. WALCOTT, 1884, U. S. Geol. Survey Bull. 10, p. 23, pl. 2, figs. 3, 3a.
Microdiscus dawsoni Hartt. MATTHEW, 1886, Trans. Roy. Soc. Canada, vol. 3, pt. 4, p. 75, pl. 7, figs. 11a–c.
Microdiscus dawsoni Hartt. MATTHEW, 1896, Trans. New York Acad. Sci., vol. 15, p. 240, pl. 17, figs. 5a–e.
Goniodiscus dawsoni (Hartt). RAYMOND, 1913, Ottawa Nat., vol. 27, p. 101, fig. 14.
Calodiscus dawsoni (Hartt). HOWELL, 1935, Jour. Paleontology, vol. 9, p. 225.
Dawsonia dawsoni (Hartt). RESSER, 1937, Smithsonian Misc. Coll., vol. 95, no. 22, p. 8.
Dawsonia spinifera KOBAYASHI, 1943, Proc. Imp. Acad. Tokyo, vol. 19, p. 39.
Dawsonia spinifera KOBAYASHI, 1944, Jour. Fac. Sci. Imp. Univ. Tokyo, sec. 2, vol. 7, pt. 1, p. 59, pl. 2, fig. 17a–b.
Dawsonia dawsoni (Hartt). KOBAYASHI, 1944, Jour. Fac. Sci. Imp. Univ. Tokyo, sec. 2, vol. 7, pt. 1, p. 59, pl. 1, figs. 9a–b.

Available material.—Hartt's types, presumably preserved in the Cornell University collections, could not be found. However, abundant topotype material is available. This includes numerous specimens, probably collected and identified by Hartt, now in the U. S. National Museum; a complete shield identified by Matthew; another complete shield from the collections of Princeton University; and abundant material collected by the writer at Fossil Brook, New Brunswick.

All the known specimens of this form are preserved in the olive-green, fine-grained, siliceous shale of the Fossil Brook formation (Hayes and Howell, 1937). The test is not preserved, or at most represented by a powdery, ferruginous residue. However, internal casts and external impressions show all the details of the surface ornamentation. The specimens from St. John underwent considerable flattening. Those from Fossil Brook preserve most of the convexity but show distortion.

Description.—The species was but briefly described by Hartt, but sufficient supplementary descriptions by Walcott and Matthew make repetition unnecessary.

Matthew (1896) mentions that the thorax consists of two segments. Two complete shields examined and figured here unquestionably confirm this statement.

Remarks.—The species is the only one of the genus found in North America. *Dawsonia spinifera* was based by Kobayashi on Matthew's specimens, separated from *dawsoni* by misleading features of the poor illustrations given by Dawson and Matthew. *Dawsonia canadensis* Kobayashi is a young pygidium of *Eodiscus scanicus* as pointed out in decribing that species.

Horizon and locality.—Middle Cambrian; Fossil Brook formation (*Paradoxides eteminicus* zone). Type locality St. John (Seely Street), New Brunswick. Other localities Fossil Brook, Hanford Brook, and Ratcliff Brook, New Brunswick.

Types.—Syntypes: Cornell University (possibly lost). Plesiotypes: ROM 556; PU 73549; USNM 14866, 18192, 116354–5.

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FOSSIL SNAKES AND LIZARDS FROM THE LOWER MIOCENE OF FLORIDA

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ABSTRACT—Three species of snakes, based on vertebrae, and one lizard, based on a fragment of mandibula, are described from the Thomas Farm deposits. All the snakes are assigned to the family Boidae; one is a new species of *Ogmophis* and the remaining two new species of *Neurodromicus*, a genus hitherto assigned to the Crotalidae. The lizard is provisionally referred to the anguid genus *Peltosaurus*. The relationships of this fauna seem to lie rather in the Oligocene than in the Recent.

INTRODUCTION

AMONG the abundant material of mammals collected at Thomas Farm, Gilchrist County, Florida, for the Museum of Comparative Zoölogy, Harvard University, there are some remains of snakes and lizards that deserve description.

The interest of this fauna lies chiefly in the paucity of Miocene *Squamata* in North America and on its comparison with the Tertiary faunas of the West.

The Thomas Farm beds are usually referred to the Arikareean, lower Miocene; discussions of the chronology of the deposits and of the correlations of the mammalian fauna are to be found in Romer (1948) and White (1942).

SERPENTES

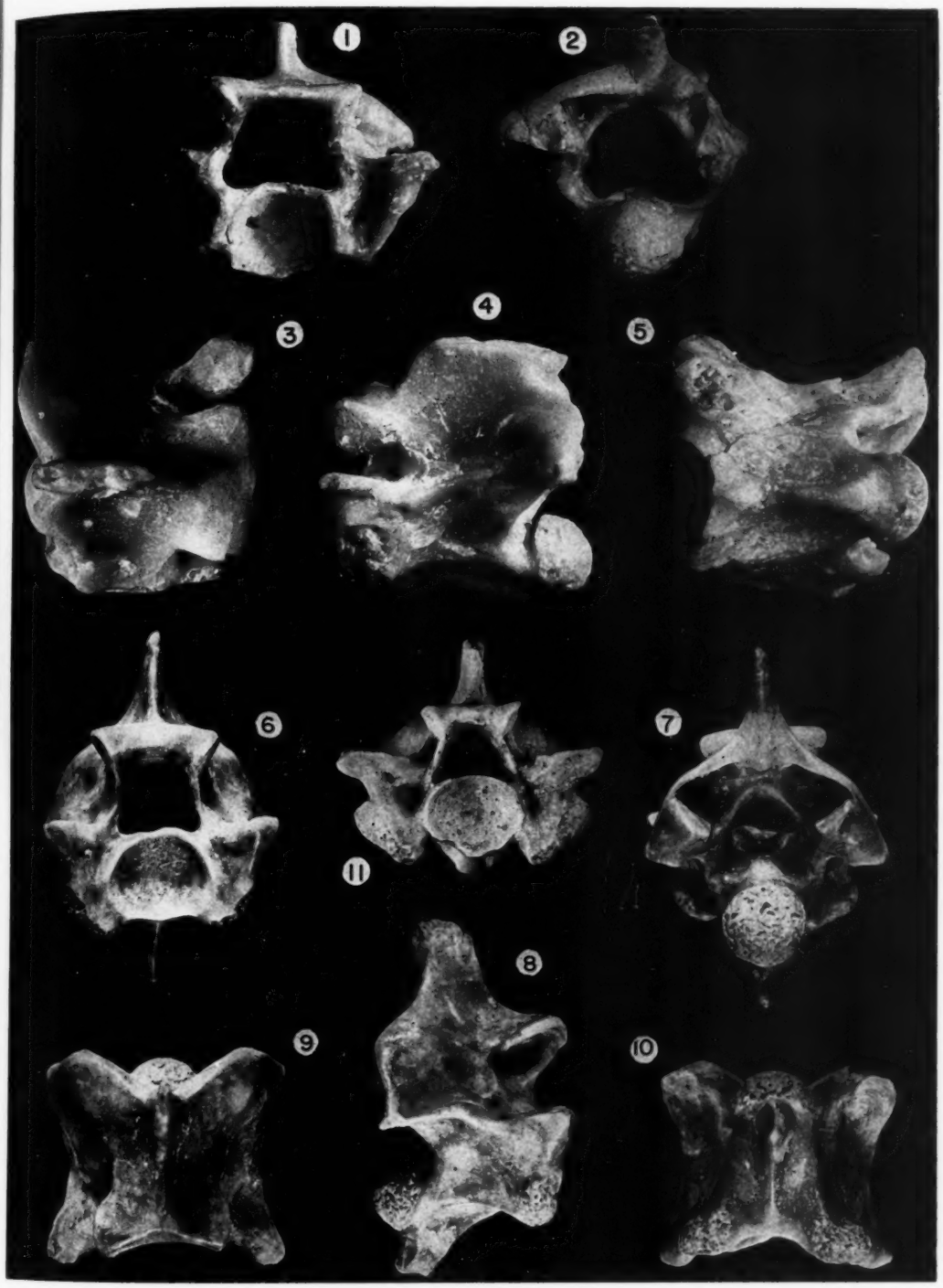
Three species of snakes, all represented by vertebrae, are recognizable in the Thomas Farm material. They are here assigned to the family Boidae. It is customary to attribute to this family the fossil snake vertebrae presenting the following characters: a) centrum short, little tapering; b) no aberrant processes of the zygapophyses and diapophyses; c) zygosphene relatively massive. These characters, although present in Recent boids, do not completely warrant acceptance of the family assignment. This will depend on the eventual demonstration of cranial characters. Unfortunately, skulls of fossil snakes are exceedingly rare, and the few available do not afford decisive evidence.

The fossil snakes of North America attributed to the family Boidae are placed by Gilmore (1938) into three genera: *Boavus* Marsh (Eocene), *Ogmophis* Cope (Oligocene and Miocene) and *Calamagras* Cope (Oligocene).

Boavus is characterized by the high neural arch and very heavy zygosphene. The lower jaw and quadrate of the genotype, *B. occidentalis* Marsh and an incomplete and partially dissociated skull of *B. idelmanni* Gilmore are known. The quadrate of *B. occidentalis* does not resemble that of the Recent boids, being decidedly narrowed at the lower end. The lower jaw of the same species, of which only the lingual aspect has been uncovered, presents the splenio-surangular suture very much like that of the Recent boids. The element indentified as a coronoid, however, is very dubiously that. The lower jaw of *B. idelmanni* closely resembles that of *B. occidentalis* and likewise does not furnish any evidence of the presence of a coronoid bone. The sagittal crest resembles that of modern boids, but the prefrontal (if correctly identified) is distinctly colubroid in appearance, being connected with an anterolateral facet of the frontal and not medially prolonged, as is the case in the modern boids.

EXPLANATION OF PLATE 55

FIGS. *1–5*—*Ogmophis pauperrimus* Vanzolini, n. sp. Holotype, ×7.6. (p. 453)
6–11—*Neurodromicus stanolseni* Vanzolini, n. sp. *6–10*, Holotype, ×5. *11*, A posterior vertebra, ×5. (p. 455)



Vanzolini, Florida Miocene snakes and lizards

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Ogmophis and *Calamagras* are genera of smaller snakes, with a characteristic low and long neurapophysis and a thin zygosphene. *Ogmophis* presents a ridge from the parapophysis to the vicinity of the condylus: this ridge is absent in *Calamagras*. There is doubt about the value of this distinction. It seems to me, however, that this ridge is a constant character when present, appearing in all the vertebrae of the individual.

It might be well to remark at this point that many related Recent species are indistinguishable on the basis of vertebral characters. I could not assemble sufficient material of Boidae to perform a comparative study of the subject with allowance for individual variation, but I have no doubt the concept of species when applied to fossil snakes widely differs from that applied to Recent ones.

One small vertebra from Thomas Farm can be assigned without doubt to the genus *Ogmophis*, and is here described as the type of a new species. A complete comparison with the remaining species of the genus, which are of themselves very poorly known, is of course not possible. The generic assignment, however, seems to be indubitable, and there is reason to believe that additional material will stress, rather than weaken, the morphological differences here pointed out.

OGMOPHIS PAUPERRIMUS Vanzolini, n. sp.
Plate 55, figures 1–5

Material.—One dorsal vertebra, MCZ 1976 (holotype).

Description of the holotype.—Small dorsal vertebra, missing both zygapophyses of the right side, otherwise well preserved. Centrum short, little tapering. Neural arch considerably flattened, distinctly emarginated between the pre- and the postzygapophyses. Neurapophysis low, occupying three-fourths of the length of the neural arch, reaching a little beyond its posterior margin. Zygosphene very flat, a little wider than the glenoid cavity, with a small swelling on the anterior lip. Neural canal relatively broad and high, epapophysis distinct. Prezygapophysis markedly oblique to the midline. Postzygaphophysis thin. Zygantrum very wide and low. Glenoid cavity elliptical. Diapophysis eroded, auriculiform, in line with the lower margin of the diapophysis. Condylus oblique, with a distinct neck. Hypapophysis reduced to a low ridge, swollen behind. A distinct ridge from the parapophysis to the condylus.

Taxonomic discussion.—This vertebra differs markedly from the known species of *Ogmophis*. It is practically impossible to compare *O. pauperrimus* with the genotype, *O. oregonensis* Cope, since the type material of the latter species (from the John Day, upper Oligocene of Oregon) is missing (Gilmore, 1938: 37) and the published figures are rather poor. It seems, however, that the emargination of the crest between the zygapophyses is much less accentuated in *O. oregonensis*.

From *Ogmophis arenarum* Douglass, a species from the Flint Creek beds, upper Miocene of Montana, and apparently the nearest relative, the new form differs chiefly by the relative width of the zygantrum (wider in the new form) and by the shape of the emargination on the ridge between the zygapophyses, which is rounded in *arenarum* and angular in *pauperrimus*. This comparison, as well as the next, was based on Gilmore's (1938) figures of the types of Douglass' and Lambe's species.

From *Ogmophis compactus* Lambe, a species from the Oligocene of Saskatchewan, *O. pauperrimus* differs in many respects, especially in general proportions, relative length of the basis of the neurapophysis, shape of the zygantrum, etc.

From *Ogmophis angulatus* (Cope), of which I have seen the type, it differs chiefly in the shape of the neural arch, strongly tilted forward in Cope's species, which was probably collected in the *Oreodon* beds of

EXPLANATION OF PLATE 56

FIGS. *1–5*—*Neurodromicus barbouri* Vanzolini, n. sp. Holotype, ×4. (p. 455)
6—*Neurodromicus barbouri* Vanzolini, n. sp. Paratype, showing neurapophysis, ×5. (p. 455)
7, 8—*Peltosaurus floridanus* Vanzolini, n. sp. Holotype, ×4. (p. 457)
9—Unidentified lizard femur, ×3. (p. 457)

Cedar Creek, Colorado (Gilmore, 1938).

From the two species to be next described the main qualitative differences are in the shape of the neurapophysis and of the zygantrum.

The two other species of snakes that I recognize in the Thomas Farm material were initially hard to place. They are very distinct from one another, but present nevertheless features in common that permit one to form a good idea of the generic characteristics.

They do not fit in *Boavus* (which one of them resembles in size) because of the very different shape of the neural arch and lesser thickness of the zygosphene. Again the shape of the neural arch and especially of the neurapophysis separates them from the species of *Ogmophis*, while the possession of a strong ridge from the parapophysis to the vinicity of the condylus does not favor inclusion in *Calamagras*. The only European genus they seem to approach is *Scaptophis*, which is separable on strength of the neural arch and of the neurapophysis. No marked resemblance was found to modern forms.

Searching other families and genera *incertae sedis* for a good fit, this was found with a form placed by several authors, including Gilmore (1938), in the Crotalidae. This is *Neurodromicus dorsalis* Cope, 1873, genus and species based on one vertebra from the *Oreodon* beds of Cedar Creek, Pawnee Buttes, northeastern Colorado. Cope's original description runs as follows:

> Char. gen. Centrum small, with a prominent truncate hypapophysis. Neural arch capacious, the zygantrum wider than the articular cup. Neurapophysis bounding the canal laterally below the zygosphene; its border not angulate behind. Parapophysis projecting acutely below centrum. An elevated neural spine.
>
> Char. specif. Articular surface of centrum round; the ball with a slight upward-looking obliquity. Hypapophysis continued to cup as a prominent carina. A ridge connecting the zygapophyses. Neural spine extending its base forward, so as to stand on the entire length of the neural arch. Measurements . . .
>
> The zygantrum is capacious, and the whole neural arch open and light. The species was about the size of the black snake (Bascanium constrictor).

Gilmore (1938: 76) directed attention to "Crotaline resemblances such as the presence of a compressed hypapophysis, paired parapophysis projecting acutely below the centrum and plate-like spine" but only cautiously endorsed the family assignment, originated by Hay (1902), professing to maintain it until "discovery of additional materials shall disclose its true family affinities." Furthermore, Gilmore stresses the enormous gauge of the neural canal in Cope's specimen.

Of all the characters cited above only one would be really important as showing crotalid affinities: the projecting parapophyses. Gilmore's own figure of Cope's type, however, discloses that the parapophyses of *Neurodromicus dorsalis* are much more reduced than those of *Crotalus*, reaching about the same extension as seen in the boids. Examining Cope's type, and to date the only specimen, of *N. dorsalis* under good optical instruments, I realized that one of the diapophyses is chipped off, creating the impression of an acute process. The contralateral one, however, is rounded and of very good boid type.

Careful comparison of the Thomas Farm material with the type of *N. dorsalis* led to the conclusion that several very strong resemblances, particularly in the shape of the neural arch and of the articular surfaces, existed between them. On the other hand, two differences were found: the gauge of the neural canal and the extension of the neurapophysis.

It is known that in snakes the most anterior vertebrae have extremely large neural canals. Examination of skeletons of *Boa*, *Constrictor*, *Python* and *Eryx* revealed that the structure of the type of *N. dorsalis* is characteristic of a very anterior dorsal vertebra of a boid snake. Comparing the vertebrae from Thomas Farm with skeletons of *Boa*, of which some were available, thanks to the kindness of Mrs. B. M. Hecht, of the American Museum of Natural History, it was possible to verify that the type of *N. dorsalis* bears to the type of one of the species to be described below (the most anterior vertebra of the lot) the same relationship that a very anterior dorsal vertebra of *Boa* bears to one situated 10 to 20 vertebrae behind itself.

For these reasons I propose to place the genus *Neurodromicus* in the family Boidae, as defined by vertebral characters, with the following amended diagnosis:

Genus NEURODROMICUS Cope, 1873

Type species: *N. dorsalis* Cope, 1873 (monobasic).

Diagnosis.—Boidae, vertebrae having centrum short; hypapophysis high and compressed in the anterior dorsals, reduced to a ridge posteriorly; neural arch characteristically convex near the midline; neurapophysis high and oblique; condylus oblique; a ridge from parapophysis to the vicinity of the condylus; parapophysis slightly projecting below the centrum.

NEURODROMICUS DORSALIS Cope, 1873

COPE, 1873, p. 15.

Holotype.—American Museum of Natural History no. 1599.

Type locality.—Cedar Creek, Pawnee Buttes, northeastern Colorado.

Horizon.—*Oreodon* beds, Oligocene.

NEURODROMICUS STANOLSENI
Vanzolini, n. sp. Plate 55, figures 6–11

Material.—Nine vertebrae.

Description.—Holotype, MCZ 1977 Complete and very well preserved vertebra from an anterior level of the column. Centrum short and little tapering. Neural arch relatively high but not heavy; neural canal wide; epapophysis distinct. Neurapophysis occupying the posterior three-fourths of the neural arch, high, inclined backwards. Zygosphene not heavy, with front lip slightly arched, devoid of tubercle. Prezygapophysis not very prominent, making an almost imperceptible angle with the diapophysis; articular surface of the prezygapophysis characteristically elongated obliquely to the midline. Postzygapophyses broad and heavy, assuming together with the posterior aspect of the neural arch a strongly arched outline quite characteristic of the genus. Zygantrum narrow and deep. Glenoid cavity elliptic. Diapophyses slightly worn, showing, however, that the articular surface is continuous, auriculiform. Condylus round in outline, distinctly oblique, with an extremely short neck. Hypapophysis beginning as a low but sharp ridge at the rim of the glenoid cavity, running back and downward. A distinct ridge from the parapophysis to the vicinity of the condylus.

Variations of the paratypes.—One of the paratypes MCZ 1977; plate 55, fig. 11 is an anterior dorsal and closely resembles the type in all respects except two: the hypapophysis is shorter and the prezygapophyses are more prominent, causing the vertebra to look lower and wider and forming a more distinct angle with the diapophyses.

All the remaining paratypes are posterior vertebrae. Two of them are large, looking more massive than the type. They agree with it in all respects but in being shorter and broader, having a smaller neural canal and having the hypapophysis reduced to a low keel. The remaining vertebrae, much smaller, confirm the characters of the two above mentioned without discrepancy. The only thing to be noticed is that one of the smaller ones has the glenoid cavity quite angular in outline.

From the examination of these various vertebrae of widely different sizes and pertaining to different regions of the column, we are in a position to judge the value of the taxonomic characters involved. It has been found that the characteristic arching of the neural arch, the shape of the neurapophysis, of the condylus and especially of the articular surface of the prezygapophysis are very constant in all the specimens.

The species is named after Mr. Stanley J. Olsen, who assembled the material studied.

NEURODROMICUS BARBOURI
Vanzolini, n. sp. Plate 56, figures 1–6

Material.—Five vertebrae.

Description.—Holotype, MCZ 1978. A vertebra complete but for the neurapophysis, broken at the base. Centrum short and little tapering. Neural arch rather flat; neural canal low; epapophysis distinct. Zygosphene heavier than in *N. stanolseni*, with a slight tubercle in the front lip. Prezygapophysis prominent, forming a sharp angle with the diapophysis; articular surface of the prezygapophysis triangular in outline, with the front side perpendicular to the median line. Postzygapophyses very heavy. Zygantrum relatively narrower than in *N. stanolseni*. Posterior outline of neural arch and zygapophyses flatter than in the former species. Glenoid cavity almost perfectly

round. Diapophyses almost not eroded, auriculiform, with the upper half concave and the lower half nearly plane. Condylus of characteristic shape, slightly pointed above, distinctly oblique, with a short neck. Hypapophysis low and more or less rounded, ending in a blunt, swollen tip. A distinct ridge from the rim of the glenoid cavity to the vicinity of the neck of the condylus.

Variations of the paratypes. Plate 56 fig. 6. —One anterior vertebra MCZ 1978 of which the posterior part of the neural arch and the neurapophysis are destroyed shows clearly a short, blunt hypapophysis, of which the posterior margin is almost perpendicular and that reaches in front the rim of the glenoid cavity (as in all the remaining specimens).

Another partially destroyed vertebra presents the neurapophysis well preserved (fig. 6); it is high and thick. The two remaining vertebrae are interesting in having the glenoid cavity elliptical.

From the consideration of this material it is possible to infer as to the more constant characters of *N. barbouri*. The shape of the condylus, the small tubercle of the anterior lip of the zygosphene and the outline of the articular surface of the prezygapophysis seem to be reliable characters.

This species is named after the late Thomas Barbour, whose characteristic foresight and generosity made possible the exploration of the Thomas Farm pit.

Comparison between N. stanolseni *and* N. barbouri.—Size is a first distinction between the two species. Several individuals (perhaps as many as the number of vertebrae available, as two have not been found together) are certainly present in the sample at hand. *N. barbouri* seems a decidedly larger species. There is, however, overlap in size, as the two largest vertebrae of *N. stanolseni* equal in size the two smallest of *N. barbouri*. As these vertebrae belong, furthermore, to the same general region of the vertebral column, I believe a comparison of them is the most adequate check on the distinctness of the two forms.

The easiest way of telling them apart is by means of the articular surface of the prezygapophysis (figs. 9 and 4). Another trait is the angle formed by the prezygapophysis and the diapophysis (figs. 11 and 1). The neural arch is definitely lower in *N. barbouri* (figs. 8 and 3, pls. 55 and 56).

TABLE 1.—MEASUREMENTS OF SNAKE VERTEBRAE (IN MM.)

	N. stanolseni							*N. barbouri*					*O. pauperrimus*
Length of centrum and ball	5.2*	5.7	5.7	4.6**	4.3	4.2	4.1	8.8*	9.2**	9.8	6.7		4.0
Height from lower rim of cup to top of zygosphene	6.1	7.3	7.2	4.9		4.6		10.4	9.3	10.5			3.7
Width at prezygapophyses	7.6	0.1	9.2	8.2	7.3	6.7	5.5	17.1		17.0		12.2	
Width at postzygapophyses	7.6	9.8	0.4	7.3	7.6	6.4		15.9					
Thickness of zygosphene	0.7	1.2	1.2	0.5	0.4	0.3	0.5	1.2		1.8	1.2	1.1	0.1
Width of zygosphene	3.7	4.9	4.7	2.9	3.0	2.9	3.1	5.5	5.4		5.2	5.3	3.1
Width of zygantrum	5.2	5.5	5.3	3.5	4.3	4.0	3.6	5.8					
Distance between parapophyses	3.7	4.9	4.9	4.0		2.5		6.7		6.4		4.3	3.0
Height of neurapophysis	3.1	3.7	2.4	2.1		1.5			4.0		3.7	4.0	1.0
Height of hypapophysis	2.4					1.5							1.0
Height of hypapophysis	2.4					1.5				3.1			
Width of cup	2.8	3.8	4.4	3.1	3.7	2.7		5.5	4.3	4.9			2.1
Height of cup	3.1	3.4	3.7	2.4		2.6	2.7	5.5	5.5	6.5			1.8

* Holotype.
** Figured specimen.

Taxonomic discussion.—I would not like to venture any opinion on the classification of the fossil boids, for two major reasons. One is that they are poorly known, and the second is that our knowledge of the vertebral morphology of the Recent forms is shamefully inadequate and insufficient for any extrapolation to the fossil data. In a general way it seems to me that *Neurodromicus* is a genus that fits well into the pattern of the Eocene-Miocene assemblage of fossil boids, closer perhaps to *Boavus* than to anything else. I do not see any suggestive resemblances with the Recent genera, having compared it with *Eunectes, Constrictor, Boa, Python, Eryx, Lichanura* and *Charina*. Special attention was given to a comparison with the two last named genera, the only Recent North American boids. No

resemblances were found beyond the family level.

SAURIA

Two fragments of jaws and a broken femur found at Thomas Farm are ascribable to lacertilians. One of the jaw fragments presents enough characters for discussion and is here described as the type of a new species.

PELTOSAURUS FLORIDANUS
Vanzolini, n. sp.
Plate 56, figures 7, 8

Material.—Fragment of a right mandibula.

Description.—Holotype: MCZ 1979, plate 56 figs. 7–8 a fragment of right mandibula, measuring 14 mm.; reaching in front of the insertion of the fourth tooth from the back and behind the vertical of the posterior margin of the masseteric process of the coronoid bone. Only tooth preserved (third from the back) pleurodont, with cylindrical and laterally compressed, slightly dilated, straight-edged, faintly wrinkled (somewhat worn) crown. Surangular fitting into a notch of the dentary, not reaching the anterior angle of the dentary process of the coronoid. Angular showing more on the buccal than on the lingual side, not large. Dentary processes of coronoid well developed, the medial longer than the lateral. Masseteric process of coronoid with anterior margin turned outward and posterior inward. Splenial reaching the vertical of the posterior margin of the masseteric process of the coronoid, between the angular and the surangular.

Taxonomic discussion.—The characters of the only preserved tooth point to some of the families of *Anguimorpha* and *Scincomorpha*. This last named group is dismissed on account of the smallness of the angular bone. Comparing the sutural pattern of the fragment of jaw at hand with equivalent material of fossil and Recent North American and European *Anguidae*, I found that a satisfactory match is found in *Glyptosaurus* and *Peltosaurus*. In none of them, however, does the lateral dentary process of the coronoid reach so far in front. This character indubitably separates the new species from all known forms of *Peltosaurus* and *Glyptosaurus*; it may even mean more than that, placing the new species in a different genus. I am not, however, prepared to take this course on such incomplete material and prefer to assign the species to *Peltosaurus*, which it seems to resemble more closely and which is stratigraphically plausible. It must be noticed that no dermal scutes, so abundant in the fossil anguids, were found in the Thomas Farm beds. But the scarcity and scatter of the material do not encourage one to draw any inferences from this fact.

The remaining fragment of jaw and the upper half of a femur (plate 56, fig. 9) are beyond my capacity of identification, so I prefer not to assign any names to them.

MANUSCRIPT RECEIVED APRIL 27, 1951

ACKNOWLEDGMENTS

I wish to thank Dr. A. S. Romer, who furnished the material and the facilities for this work, and Mr. Stanley J. Olsen, for his interest in the problem, both in the laboratory and in the field. I had occasion to examine material in the collections of the United States National Museum, American Museum of Natural History and Princeton University, to whose authorities I am indebted.

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JOURNAL OF PALEONTOLOGY, VOL. 26, NO. 3, PP. 458–483, PL. 57, 5 TEXT FIGS., MAY 1952

PALEONTOLOGY OF NORTHWESTERN VERMONT

II. FAUNA OF THE UPPER CAMBRIAN ROCKLEDGE CONGLOMERATE NEAR ST. ALBANS

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ABSTRACT—The fauna of the matrix and pebbles of the Rockledge conglomerate is redescribed. Eight species not previously noted are recorded; six names previously used are suppressed, and the presence of five species previously reported is not confirmed. The fauna comprises 17, or possibly 18, trilobites and a gastropod. The Rockledge is regarded as belonging to the *Cedaria* zone.

It is suggested that the cheirurid subfamily Sphaerexochinae descended from the corynexochid Catillicephalinae. Summaries are given of the smooth Upper Cambrian trilobites and of the Menomoniinae, of which the Nepeidae are suppressed as a synonym.

INTRODUCTION

THE Rockledge is a locally prominent, discontinuous limestone conglomerate of Dresbachian age. Although early recognized as a mappable unit its age was long a matter of dispute. It was first included by Hitchcock and others (1862, map) in the "Georgia formation," a unit embracing Lower, Middle, and Upper Cambrian and Lower Ordovician rocks. Later, Walcott (1887) placed it near the center of his "Georgia section," which was for many years regarded as the standard for the Lower Cambrian.

In 1923, Keith grouped all limestone conglomerates in northwestern Vermont in the "Swanton conglomerate," erroneously including both Cambrian and Ordovician beds. Later, the Rockledge was included in the "Corliss conglomerate" (Keith, 1932, p. 378; Schuchert, 1933, pp. 378–379), and the name "Swanton" was abandoned. But when it was discovered that the type Corliss was Lower Ordovician (Raymond, 1937, pp. 1140–1141), whereas the Rockledge was Upper Cambrian (op. cit., pp. 1135–1140) Schuchert (1937, p. 1049) proposed the name "Rockledge limestone breccia" for the Dresbachian part of the old Corliss and confined the latter name to conglomerates now included in the Morses Line slate (Shaw, 1951, p. 98).

The type locality is on the Rockledge Estate, 4.4 miles north of St. Albans on the west side of the St. Albans-Highgate Falls road. I have designated these outcrops SA-EC-17, for they were the seventeenth fossiliferous exposure discovered in the east-central ninth of the St. Albans quadrangle (Fig. 49). Pebbles from this locality are designated by letter or number and assigned to Locality SA-EC-17P.

The majority of fossils from the matrix have been found in the basal sandy limestone and calcareous sandstone 3½ miles north of St. Albans on the west side of the same road (Locality SA-EC-16 of this report). This site has been partly figured by Schuchert (1937, pl. 6, fig. 1), who called it Loc. XIII in the legend of his figure, Loc. XIV on the map (p. 1004), and Loc. 1 in Table 2 (p. 1051).

The southernmost exposures of the Rockledge in the St. Albans quadrangle are at Mayre's Ledge, two miles south of St. Albans. Only the pebbles have yielded fossils here (SA-SC-13P). Unfortunately, access to these outcrops is denied so that collections from them are small.

STRATIGRAPHY

A full discussion of the stratigraphy of the St. Albans area, together with an areal map, is now in preparation so only an outline need be given here.

The Dresbachian formations of the St. Albans area are, from below upward, the Mill River conglomerate, Skeels Corners formation, Rockledge conglomerate, and Hungerford slate. All are provisionally assigned here to the *Cedaria* zone.

The Rockledge lies above the Skeels

Corners with an angular unconformity and is gradational upward into the Hungerford slate. The thickness ranges from zero to 100 feet and averages about 30 feet, with the thickest section lying just north of the type locality. At the base of the formation there is commonly a non-conglomeratic arenaceous dolomite or limestone, which thickens irregularly from four feet in the northern part of the Milton quadrangle to a maximum of 50 feet north of the Rockledge estate. Above this sandy layer are the conglomerates, composed of a matrix of dark-blue, highly arenaceous limestone containing fragments of unfossiliferous pale-blue or gray limestone ranging in size from small pebbles to boulders nearly 100 feet long. Smaller pebbles of dark-gray slabby limestone and of dark-gray massive limestone are less common, but they have yielded all of the fossils taken from pebbles.

ACKNOWLEDGMENTS

The types of all species were studied except those of *Acrohybus argutus* and *Leiocoryphe? prisca*. Through the kindness of Dr. Carl O. Dunbar I was permitted to make casts of the Rockledge types in the Yale Peabody Museum, and I am also indebted to him for the photographs of *Stenelymus kobayashii* and of the plesiotype of *Maryvillia* reproduced here, as well as for the loan of types.

Dr. Franco Rasetti kindly reviewed and criticized the completed manuscript and gave valuable suggestions on classification. He also called my attention to specimens in the National Museum reputedly from the Rockledge, but because of the poor locality data with them they were not studied.

I have had at my disposal the collection from the Rockledge in the Museum of Comparative Zoölogy, which includes some types, as well as specimens collected by myself during 1947 and 1948.

Finally, I wish to express my sincere appreciation to Miss Joan Lund for her typing of the final manuscript.

THE FAUNA

The distribution of the fauna is given in Table 1. A few inarticulate brachiopods were found and set aside for further study, but with this exception the entire known fauna is discussed on the following pages.

FIG. 1—Locality SA-EC-11, on the Rockledge estate, but not assigned to the Rockledge conglomerate. Looking north.

There are differences between the pebble and matrix faunas, as is to be expected, but both are certainly Dresbachian. Lochman and Duncan (1944, p. 35) suggest that the Rockledge should be assigned to the *Crepicephalus* zone, but the present revision of generic assignments and elimination of repetitive names seems to indicate that the formation belongs to the *Cedaria* zone.

Unfortunately, there are no fully reliable guides to either zone present in the matrix. *Blountia*, *Coosia*, and *Meteoraspis* range through both zones, although *Meteoraspis* is said to be more common in the *Cedaria* zone (Lochman and Duncan 1944, p. 41). Probably the best indication of the age is given by *Welleraspis*, which is represented by an unnamed species; this genus is regarded by Lochman (1938, pp. 462–463) and Howell (1945, p. 30) as of *Cedaria* age alone. The pebbles are probably of only slightly greater age than the matrix.

A LOCALITY NOT INCLUDED IN THIS REVISION

There is on the Rockledge estate an outcrop of conglomerate formed of slabby, thin-bedded, pale-blue limestone pebbles in an arenaceous limestone matrix (Text-fig. 1). It is fossiliferous and has been designated Locality SA-EC-11, but the fauna of this outcrop is not included because:

(1) The cleavage in the outcrop is at variance with that of the surrounding rocks to a degree that suggests that the outcrop is a glacial erratic. (2) Nowhere in undoubted exposures of the Rockledge have pebbles of

this particular shape and color been seen in such numbers. The entire outcrop is lithologically distinct. (3) The fauna is not ilke that collected elsewhere in the Rockledge. It is dominated by the form described herein as *Acheilus* n. sp., whereas only one specimen of that species is known from accepted Rockledge. *Apachia* Frederickson 1949, and *Leiocoryphe* Clark 1924, are both present, and these genera are characteristic

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EXPLANATION OF PLATE 57

Figures 16, 33, 34 made from negatives supplied by Dr. Carl O. Dunbar, Yale Peabody Museum.

FIGS. *1–5*—*Catillicephala lata* (Raymond), 1937. *1–3*. Dorsal, anterior, lateral views of typical cranidium. SA-EC-16. ×2½. YPM 18630. *4*. Paratype cephalon from Pebble 1 (SA-EC-17P) with proparian facial sutures. ×2½. MCZ 4963. *5*. Damaged paratype cranidium, with occipital furrow shallow mesially. Pebble A (SA-EC-17P). ×2½. MCZ 4953. (p. 463)

6, 7—*Catillicephala fowleri* Shaw, n. sp. *6*. Large paratype cranidium showing loss of glabellar furrows; with large unassigned free cheek. SA-EC-16. ×2½. MCZ 4979. *7*, Holotype cranidium with glabellar furrows. SA-EC-17. ×2½. YPM 18633. (p. 464)

8–10—*Meteoraspis? minuta* (Raymond), 1937. *8*, Rubber squeeze of holotype cranidium of *Coleopachys strix* (YPM 14751). Pebble 2 (SA-EC-17P). ×2. U. Wyo. IT-53. *9*, Typical medium-sized cranidium. SA-EC-16. ×2½. MCZ 4969. *10*, Rubber squeeze of holotype cranidium of *Coleopachys pisum* (YPM 14750). SA-EC-16. ×2. U. Wyo. IT-50. (p. 475)

11—Pygidium No. 6. Rubber squeeze of counterpart (MCZ 4985) of type specimen (YPM 14714) of pygidium provisionally assigned to *Meteoraspis? minuta*. Oblique view. SA-EC-16. ×2. U. Wyo. IT-63. (p. 476)

12, 13—*Bynumia leptogaster* Raymond, 1937. Both specimens from Pebble 2 (SA-EC-17P). *12*, Holotype cranidium. ×2½ YPM 14756. *13*, Rubber squeeze of paratype pygidium (YPM 14757). ×2. U. Wyo. IT-71. (p. 472)

14, 15—*Protillaenus marginatus* Raymond, 1937. Paratype cranidium from Pebble 1 (SA-EC-17P). ×2½. MCZ 4965. (p. 474)

16, 17—Pygidium No. 3. Assigned to *Protillaenus marginatus*. *16*, Plesiotype of *Marywillia triangularis*. Pebble 2 (SA-EC-17P). ×5. YPM 14741. *17*, Small specimen with short axial lobe. Pebble A (SA-SC-13P). ×2½. MCZ 4989. (p. 474)

18–20—*Welleraspis* sp. All from SA-EC-16. All ×2½. *18, 20*. Best preserved cranidium. MCZ 4971. *19*, Largest cranidium, preserving palpebral lobe. MCZ 4973. (p. 479)

21—Pygidium No. 1. Assigned to *Welleraspis* sp. SA-EC-16. ×2½. MCZ 4973. (p. 480)

22–24—*Acmarhachis* sp. *22*, Cephalon. SA-EC-16. ×2½. MCZ 4978. *23, 24*, Pygidium. SA-EC-16. ×2½ and ×13. TPM 18647. (p. 481)

25–28—*Blountia* (*Homodictya*) *imitatrix* (Raymond), 1937. *25*, Rubber squeeze of paratype pygidium of *Coleopachys strix* (YPM 14752). Pebble 2 (SA-EC-17P). ×2. U. Wyo. IT-55. *26*, Plaster cast of holotype of *Kaninia? platys* (YPM 14738). Pebble 2. ×2. U. Wyo. IT-60. *27*, Stereoscopic views of cranidium. SA-EC-16. ×2½. MCZ 4967. *28*, Rubber squeeze of holotype cranidium (YPM 14745). Pebble 2. ×2. U. Wyo. IT-69. (p. 473)

29, 30—Agnostid No. 1. *29*, Cephalon. SA-EC-16. ×2. MCZ 4983. *30*, Cephalon from Pebble A (SA-EC-17P). ×2½. MCZ 4957. (p. 482)

31, 32—Pygidium No. 2. SA-EC-17. ×12 and ×6. YPM 18641. (p. 476)

33, 34—*Stenelymus kobayashii* Raymond, 1937. Holotype cranidium. Pebble 2 (SA-EC-17P). ×6. YPM 14717. (p. 480)

35–37—*Coosia?* sp. All specimens from SA-EC-16. *35, 36*, Paratypes of *Coleopachys strix*. ×2½. MCZ 4976 and 4975. *37*, Medium-sized cranidium. ×2. MCZ 4980. (p. 478)

38—Pygidium No. 4. Assigned provisionally to *Coosia?* sp. Rubber squeeze of paratype of *Homodictya imitatrix* (YPM 14746). Pebble 2 (SA-EC-17P). ×2½. U. Wyo. IT-68. (p. 479)

39—Free cheek No. 1. Unassigned. Largest fossil found in Rockledge conglomerate. Pebble A (SA-EC-17P). ×1. MCZ 4952. (p. 481)

40, 41—Pygidium No. 5. Unique unassigned specimen. SA-EC-16. ×2½. MCZ 4985. (p. 472)

42—*Leiocoryphe? prisca* Rasetti, 1944 (?). Cranidium assigned to species. SA-EC-17. ×2½. YPM 18627. (p. 470)

43—"*Idahoia*" *minor* Raymond, 1937. Rubber squeeze of holotype (YPM 14743). SA-EC-16. ×2. U. Wyo. IT-58. (p. 480)

44—*Bolaspidella macgerriglei* (Raymond), 1937. Paratype cranidium. SA-EC-16. ×2½. MCZ 4984. (p. 478)

45—*Hypseloconus*. Unique specimen. Pebble A (SA-EC-17P). ×6. MCZ 28003. (p. 482)

46–48—*Kingstonia* (*Kingstonia*) *scrinium* (Raymond), 1937. *46*, Exfoliated pygidium. Pebble A (SA-EC-17P). ×2. MCZ 4959. *47, 48*, Assigned, exfoliated cranidium. SA-EC-16. ×2½. YPM 18626. (p. 472)

49—Rockledge conglomerate at the type locality. SA-EC-17 and SA-EC-17P. Looking northwest. (p. 458)

Shaw, Cambrian Rockledge fauna from Vermont

of younger rocks than those of the *Cedaria* zone. However, the outcrop has been discussed in detail and is figured because it is a potential source of confusion. It lies in the midst of the type Rockledge exposures; it is not covered by shrubbery as is the rest of the Rockledge; and it is far more fossiliferous than the typical outcrops.

McGerrigle's boulder.—Raymond (1937, p. 1137) described the fauna of a boulder found by H. W. McGerrigle "northwest of Georgia Center" and assigned it to the what may be extraneous elements into the Rockledge fauna.

SYSTEMATIC PALEONTOLOGY

Order OPISTHOPARIA Beecher, 1897
Suborder CORYNEXOCHIDA Kobayashi, 1935
Family CORYNEXOCHIDAE Angelin, 1851
Subfamily CATILLICEPHALINAE Raymond, 1938, emended

Cephalocoeliidae RAYMOND. 1937, Geol. Soc. America Bull., vol. 48, p. 1124.

TABLE 1.—DISTRIBUTION OF THE FOSSILS

Locality	SA-EC-16	SA-EC-17	SA-EC-17P									SA-SC-13P		
Source	Matrix	Matrix	Pebble 1	Pebble 2	Pebble 3	Pebble 4	Pebble 5	Pebble 6	Pebble 7	Pebble 10	Pebble A	Pebble A	Pebble B	Pebble C
Catillicephala lata (Raymond), 1937	5C	3C, 5P	4C, 2P	1C	1C			1C		1C	1C, 1P	1C, 2P		
C. fowleri Shaw, n. sp.	2C	*3C*			1C						1C			
Acheilus, n. sp.									1C					
Distazeris simplex (Raymond), 1937	*1C*													
Leiocrypheℓ prisca Rasetti, 1946(?)	2C	1C				(?) 1C								
Kingstonia (*Kingstonia*) *scrinium* (Raymond), 1937	1C, 2F										1P			
Pygidium No. 5	1P													
Bynumia leptogaster Raymond, 1937			1P(?)	*1C, 1P*										
Bountia (*Homodictya*) *imitatrix* (Raymond), 1937	2C, 1P			*1C, 2P*							1P			
Acrokybus argutus Raymond, 1937				*R*										
Protillaenus marginatus Raymond, 1937			*3C*											
Pygidium No. 3				1P								1P		
Meteraspisℓ minuta (Raymond), 1937	4C			*3C*			1C							
Pygidium No. 6	1P													
Pygidium No. 2		1P												
Bolaspidella macgerriglei (Raymond), 1937	1C													
Coosiaℓ sp. (including Pygidium No. 4)	6C			1P							1C			
Wellerapis sp. (including Pygidium No. 1)	4C, 3P													
Stenelymus kobayashii Raymond, 1937				*1C*							1C(?)			
"Idahoia" minor Raymond, 1937	*1C*													
Free Cheek No. 1											1F			
Acmarhachis sp.	2C, 2P													
Agnostid No. 1	1C										1C			
Hypoleconus sp.											1			

C=cranidium or cephalon.
F=free cheek.
P=pygidiuim.
R=reported by Raymond, 1937; specimen not seen.
(?)=identification doubtful.
Italics indicate type locality for species.

Rockledge conglomerate. This was the most logical correlation to make at that time, when the faunas of the Mill River conglomerate and the Skeels Corners formation were unknown, but recent collections from these two units show that there is a similarity among the faunas of all three units and McGerrigle's boulder, and it seems best to omit the boulder from the present discussion in order to avoid the introduction of

Catillicephalidae RAYMOND, 1938, Geol. Soc. America Bull., Supplement to vol. 48, p. xv.

Raymond's family is here reduced to a subfamily of the Corynexochidae, and inasmuch as the name *Cephalocoelia* Raymond, 1937, must be replaced by *Catillicephala* Raymond, 1938, as is discussed below, the subfamily name must be Catillicephalinae.

The Catillicephalinae are small opisthoparian, proparian, or amphiparian (Shaw,

1951, p. 109) Corynexochidae with an inflated glabella that comprises most of the cephalic shield. Glabellar furrows effaced in some species, but where present, the posterior pair is rectangular and cuts off a small square lobe on each side of the base of the glabella.

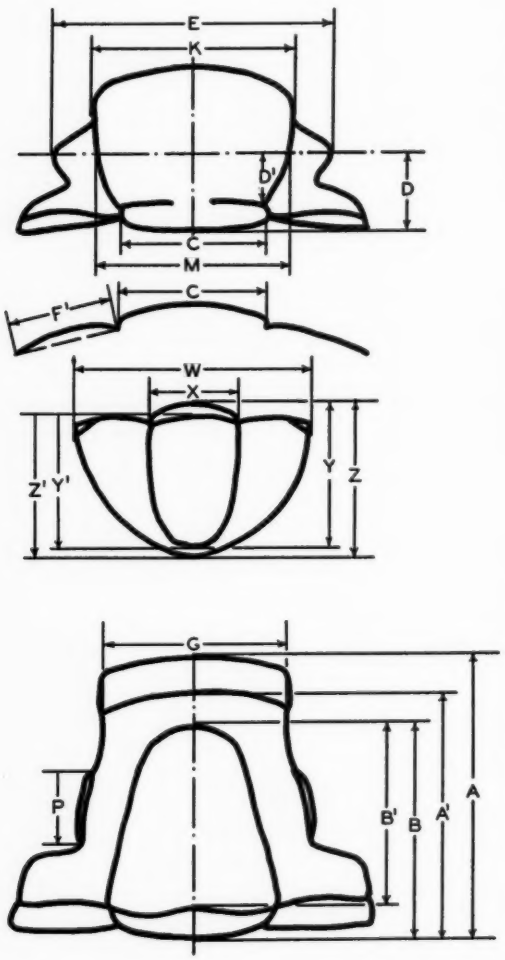

FIG. 2—Dimensions measured on trilobite cranidia and pygidia, as reported in this paper.

Pygidium short and transverse. Smooth in some genera but bearing marginal spines in others.

It seems to be possible to recognize two stocks within the Catillicephalinae. The *catillicephalid stock*, represented by *Catillicephala*, is a divergent group showing effacement of both shields. The *acheilid stock*, represented by *Acheilus* Clark, 1924, *Distazeris* Raymond, 1937, and *Madarocephalus* Resser, 1938, seems to be the main catillicephaline line in which effacement is of importance only in some species. Likewise, the members of the acheilid stock develop many cheirurid-like structures, and it is here proposed that they are the ancestors of the cheirurid subfamily Sphaerexochinae Öpik, 1937.

Table 2 lists the important features of the several generic types in the Catillicephalinae.

Catillicephalid Stock

Genus CATILLICEPHALA Raymond, 1938

Cephalocoelia RAYMOND, 1937, not Etallon, 1859, Geol. Soc. America Bull., vol. 48, p. 1124.
Ucebia RAYMOND, 1937, not Walcott, 1924 (part), op. cit., p. 1103.
Catillicephala RAYMOND, 1938, Geol. Soc. America Bull., Supplemenent to vol. 48, p. xv.
Cephalocoelia Rasetti, 1946, not Etallon, 1859, Jour. Paleontology, vol. 20, pp. 449–450.

Genotype: *Ucebia lata* Raymond, 1937 (= *Cephalocoelia ovoides* Raymond 1937).

The name *Cephalocoelia* was first used by Etallon in 1859 for a sponge, so it was not available to Raymond in 1937. Raymond's correction of the name to *Catillicephala* has been overlooked, but it should be used.

There are two available names for the genotype of *Catillicephala*. The first is *Cephalocoelia ovoides*, the cited type of *Cephalocoelia* Raymond and therefore the type of *Catillicephala*. The second is *Ucebia lata*, which I regard as a synonym of *C. ovoides*

Since the choice between synchronous synonyms is given to the first reviser I choose *Ucebia lata* because it is represented by better type material than *Cephalocoelia ovoides*.

Rasetti (1946) has given an excellent discussion of this genus and has illustrated it fully, so no further description is necessary.

Cranidia of *Catillicephala* with glabellar furrows, such as young specimens of *C. fowleri*, are not always easy to separate from cranidia of *Acheilus* because of their general similarity in structure. However, species of *Acheilus* are commonly tuberculate, while those of *Catillicephala* are smooth, except in *C. fowleri* and *C. impressa*, and the eyes of

Acheilus are at the midlength of the head, whereas those of *Catillicephala* are behind the midlength. The pygidia, of course, are very different, those of *Acheilus* being spinose.

It should be mentioned that both proparian and opisthoparian specimens of *Catillicephala lata* have been found, as individual variants. It is for this condition that the term "amphiparian" has been proposed.

This minute genus promises to be one of the best guides to the lower part of the Upper Cambrian in northeastern United States and adjoining parts of Canada. It is widely distributed and easily recognized. In the St. Albans area it is present in the Middle Cambrian St. Albans shale and the Dresbachian Mill River conglomerate, Skeels Corners formation, Rockledge conglomerate, and Hungerford slate.

CATILLICEPHALA LATA (Raymond), 1937
Plate 57, figures 1–5

Ucebia lata RAYMOND, 1937, Geol. Soc. America Bull., vol. 48, p. 1103, pl. 2, figs. 2–4 (fig. 2 is inaccurate)
Cephalocoelia ovoides RAYMOND, 1937, op. cit., p. 1124, pl. 3, fig. 22.
Catillicephala ovoides RAYMOND, 1938, Geol. Soc. America Bull., Supplement to vol. 48, p. xv.
Cephalocoelia lata RASETTI, 1946, Jour. Paleontology, vol. 20, p. 450, pl. 68, figs. 9–17.
Cephalocoelia rotunda RASETTI, 1946, op. cit., p. 450, pl. 68, figs. 18–23.

This species has been described under several names, but an examination of the specimens from the Rockledge conglomerate, including the types of Raymond's species, and from the overlying and underlying formations has convinced me that there is but one species represented. The mesial shallowing of the occipital furrow, which Rasetti regarded as peculiar to *C. impressa*, seems to be subject to intraspecific variation, for some specimens of *C. lata* show the same feature (Pl. 57, fig. 5).

The suppression of *Cephalocoelia rotunda* is, unfortunately, based only on a qualitative opinion, but the similarity of *C. lata* and *Cephalocoelia ovoides* seems to be borne out by actual measurements, given below, which have been plotted in text-figure 3. It is regrettable that the holotype of *C. ovoides* is not better preserved so that more measurements could be taken from it, but text-figure 3A suggests that the dimensions plotted fall within the limits of *C. lata*.

Catillicephala lata may be described as follows: Cephalon short and wide, dominated by a tumid glabella set high above the cheeks. Glabella overhangs front of cephalon, smooth in most specimens; rarely the rear pair of rectangular glabellar furrows is developed. Occipital furrow deep, either fully impressed or shallow mesially. No occipital node or spine. Cheeks smooth save for marginal furrow, which does not join occipital furrow. Palpebral lobes narrow, only slightly arcuate, and slightly behind the midlength of the glabella. Eyes set low on the cheeks appear to have been simple. Facial sutures amphiparian and well enough fused in many specimens to allow recovery of the complete cephalon. Genal spines not present, contrary to statement by Raymond (1937, p. 1124).

Pygidium subtriangular, nearly smooth, with prominent axial lobe. Few specimens show any trace of axial or pleural segmentation. In some individuals the axial lobe overhangs the rear margin of the shield, while in others it falls short of the margin; this variation was cited by Rasetti (1946, p. 450) as a specific feature, but intermediate stages make it appear unlikely that it can be used.

Measurements of all Rockledge specimens that are sufficiently well preserved to warrant study are given below. This tabulation does not include specimens from other formations. The measurements, in millimeters, are from the following cranidia, respectively (italicized figures are for dimensions taken on one side of cranidium and doubled): YPM 18631 from Pebble 3; MCZ 4960 and YPM 18632 from SA-EC-16; YPM 18635 and 18636 from SA-EC-17; YPM 14659, the holotype of *Cephalocoelia ovoides* from Pebble 2; YPM 18630 and U. Wyo IT-65 from SA-EC-16; MCZ 4953, a paratype of *Ucebia lata* from Pebble A at SA-EC-17P; MCZ 4963, a paratype of *Ucebia lata* from Pebble 1. The letters in parentheses after the description of the dimensions refer to text-figure 2.

Sagittal length of glabella including occipital lobe (B), 1.35, 1.8, 2.0, 2.2, 3.0, 3.3, 4.0, 4.5, 5.1, 7.3; interoccipital glabellar

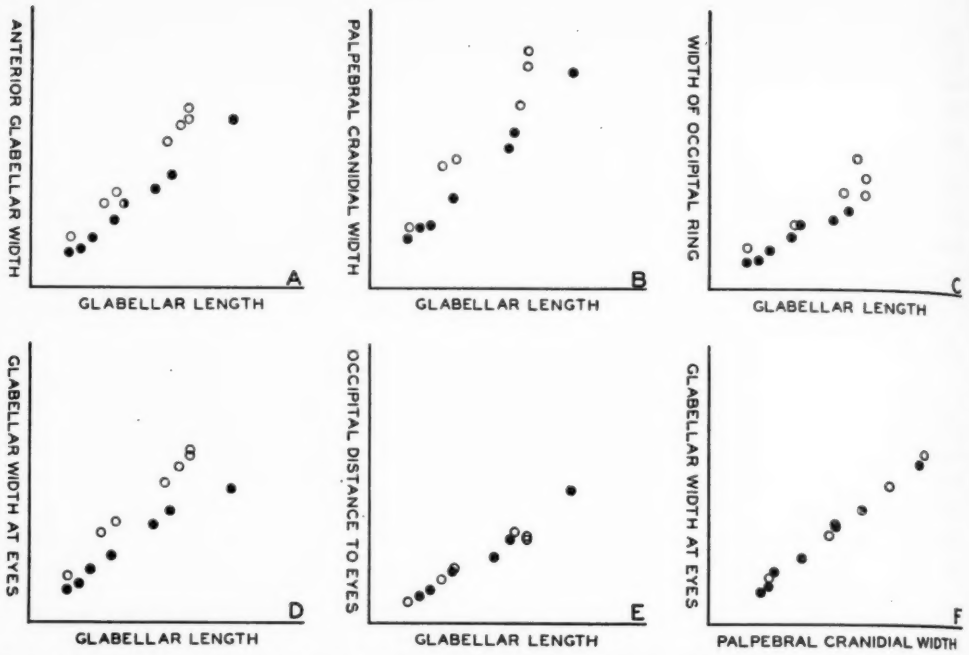

FIG. 3—Comparison of dimensions of *Catillicephala lata* (Raymond), 1937, (black dots) with those of *C. fowleri* (open circles). The half-shaded circle in A represents the holotype of *Cephalocoelia ovoides* Raymond, 1937. Dimensions as illustrated in text-figure 2. All graphs 10 millimeters on a side. See text for discussion.

length (B′), 1.05, 1.5, 1.5, 1.65, 2.5, 2.7, 3.1, 3.8, 4.2, 6.0; width of occipital ring (C), 1.0, 1.1, ——, 1.4, 1.9, 2.3, ——, 2.5, 2.8, ——; distance from centers of palpebral lobes to rear of occipital lobe, projected into sagittal plane (D), 0.75, 1.0, ——, 1.2, 1.9, ——, ——, 2.4, 3.0, 4.8; width of cranidium across centers of palpebral lobes (E), 1.9, *2.2*, ——, *2.4*, *3.4*, ——, ——, *4.6*, *6.0*, *7.8*; width of chord of posterior limb, 0.7, 0.9, ——, ——, 1.5, ——, ——, 1.8, 2.9, ——; width of glabella opposite centers of palpebral lobes (M), 1.2, *1.4*, ——, 1.9, 2.4, ——, ——, 3.5, *4.4*, *5.8*?.

Measurements, in millimeters, are given, in order, for the following pygidia: YPM 18640, 18639, 18642, and U. Wyo IT-66 from SA-EC-17; MCZ 4964 and 4964 from Pebble 1; MCZ 4952 from Pebble A at SA-EC-17P. Italicized dimensions have been doubled, as above, and letters in parentheses, refer to text-figure 2.

Maximum width (W), 2.3, *2.8*, *3.2*, 3.2, *5.4*, 5.6, 7.0; anterior width of axial lobe (X), 1.0, 1.0, 1.2, 1.4, 1.9, 2.1, 2.5; length of axial lobe, including articulating half-ring (Y), 1.7, 1.7, 2.0, 1.8, 2.8, ——, 4.0; length of pygidium, including articulating half-ring (Z), 1.7, 1.8, 2.1, ——, ——, ——, 4.1; length of articulating half-ring, 0.3, 0.2, 0.3, 0.2, 0.3, ——, 0.5.

CATILLICEPHALA FOWLERI Shaw, n. sp.
Plate 57, figures 6, 7

This species is known from seven cranidia that in many respects seem to be transitional between the typical catillicephalid form and the typical acheilid form. It is named for my fried Dr. Phillip T. Fowler, who accompanied me in the field in the summer of 1946.

The cranidium shows the fundamental generic structures, such as the large bulbous glabella, narrow fixed cheeks, and missing frontal limb, but it differs from the other described species in the combination of a wide glabella that is also straight-sided.

The glabella has a slight median longi-

tudinal keel in some individuals, but not all. Rectangular basal glabellar lobes are prominent in the smaller heads, more so than in any other species in the genus, but they disappear with increased size. The occipital furrow is shallow in the center.

C. fowleri is closest to *C. impressa* (Rasetti), 1946, which it resembles in the extreme width of the glabella, mesial shallowing of the occipital furrow, and sparsely granulated surface. The two differ in that the glabella is suboval in *C. impressa* and subtrapezoidal in *C. fowleri.*

C. fowleri seems to demonstrate more clearly than any other species, the close connection between *Catillicephala* and *Acheilus.* It is probably close to the morphologic point at which *Catillicephala* split from *Acheilus,* although the presence of smooth catillicephalines in older beds shows that *C. fowleri* is not itself the oldest species in the genus.

Measurements of the types of *C. fowleri* are given below and they have been plotted in text-figure 3 for comparison with those of *C. lata.* In text-figures 3A through 3E the length of the glabella, including the occipital ring, has been used as the independent variable. This unit is essentially the same as the total length of the cranidium in both species, and it can be used to set up rough ontogenetic series.

Text-figures 3A and 3D show that *C fowleri* has a wider glabella than does *C. lata* for a corresponding glabellar length, and text-figure 3B indicates the obvious corollary that the total head width across the eyes is greater in *C. fowleri.*

Text-figure 3C suggests that the width of the occipital ring in *C. fowleri* is slightly greater than in *C. lata* but not significantly so. This is understandable when it is realized that the occipital ring must respond to two opposing stresses; first, the tendency of the larger glabella in *C. fowleri* to widen the occipital ring, and, second, the opposite tendency of the axial lobe of the thorax to be of a constant width in a genus. Apparently the widening of the glabella, a specific feature, had only a slight effect when opposed to the resistance of the more conservative thorax, a generic—or suprageneric?—feature. The erratic dimensions of the occipital ring in the larger specimens of *C. fowleri* are due in part to the mechanical difficulty of deciding on the precise limits of this member in the available individuals.

Text-figure 3E compares the position of the eyes in the two species. Eye position is a conservative feature of the trilobite head and is, thus, a character of more than specific value. Accordingly, *C. lata* and *C. fowleri* do not differ from one another in the position of the eyes but form a single, inseparable distribution pattern.

Text-figure 3F may possibly have some bearing on the manner of growth of the glabella. In this graph the width of the cranidium between the eyes is plotted against the width of the glabella on the same line. Surprisingly enough, the plots show that the cranidial width is the same in both species for a given absolute glabellar width, although the same cranidial and glabellar widths are reached at different ontogenetic stages in the two species (text-figs. 3A, B, D). This relationship shows that, in these two species at least, the glabella expands laterally, not at the expense of the fixed cheeks but by pushing them apart. We may only speculate as to the cause of this, but it is possible that the optical apparatus in *Catillicephala* had been crowded into the minimum permissible space so that the stomach size, as reflected by the size of the glabella, could not increase at the expense of the internal organs of vision but had to displace them. It will be interesting to see whether this fixed cheek-glabella relationship is found in all genera or only in those groups with reduced fixed cheeks such as the corynexochids.

Measurements, in millimeters, were made of the following type cranidia: YPM 18638 from SA-EC-17; U. Wyo IT-64 from Pebble 3; YPM 18633, the holotype, and 18634 from SA-EC-17; MCZ 4961 from SA-EC-16; MCZ 4954 from Pebble A at SA-EC-17P; MCZ 4979 from SA-EC-16. Italicized dimensions were taken on one side of damaged specimens and doubled.

Glabellar length including occipital ring (B in text-figure 2), 1.4, 2.6, 3.1, 4.9, 5.4, 5.7, 5.7; glabellar length excluding occipital ring (B′) 1.15, 2.2, 2.5, 4.0, 4.5, 4.7, 5.0; width of occipital ring (C), *1.5,* ——, 2.3,

3.5, *4.8*, 3.4, 4.0; distance from center of palpebral lobes to rear of occipital ring projected into sagittal plane (D), 0.8, 1.6, 2.0, ——, 3.3, 3.0, 3.1; width of cranidium across centers of palpebral lobes (E), *2.2*, *4.4*, 4.6, ——, *6.6*, *8.6*, 8.0; width of chord of posterior limbs, 1.1, 1.6, 1.9, ——, 2.5, ——, 2.5; width of glabella opposite centers of palpebral lobes (M), 1.7, *3.2*, 3.6, 5.0, *5.6*, *6.0*, 6.2.

Acheilid Stock

The acheilid stock includes opisthoparian or proparian Catillicephalinae with a prominent glabella, which is parallel-sided or expands anteriorly. Glabellar furrows are present, although faint in some species. Pygidium small and short, only slightly wider than long, with short, prominent axial lobe. Pygidial margin bears short, stout spines in *Acheilus*, the only genus in the stock for which that part is known. Included genera: *Acheilus* Clark, 1924 (=*Denisia* Clark, 1924, *Acheilus* Raymond, 1924, and *Theodenisia* Clark, 1948), *Distazeris* Raymond, 1937, and *Madarocephalus* Resser, 1938.

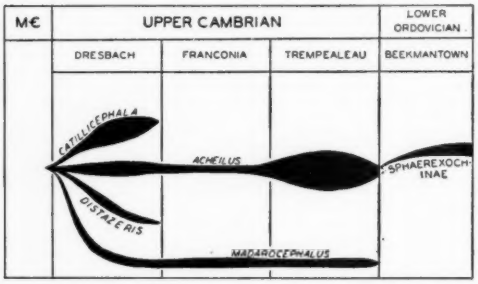

FIG. 4—Proposed phylogeny of the Catillicephalinae and the Sphaerexochinae.

It is here proposed that the acheilid stock was ancestral to the subfamily Sphaerexochinae of the family Cheiruridae Hawle and Corda, 1847. The acheilids are clearly corynexochids (Raymond, 1924, p. 422; Kobayashi, 1935, p. 131), but at the same time they show a marked tendency to develop cheirurid structures.

The following acheilid structures and phyletic tendencies appear to be homologous with those found among the Cheiruridae as a whole and among the Sphaerexochinae in particular: (1) The Catillicephalinae have developed rectangular basal glabellar furrows that isolate a pair of small basal lobes such as are found in many cheirurids, e.g., *Sphaerexochus*, *Hemisphaerocoryphe*, and *Pseudosphaerexochus*. (2) There is a tendency for the line to become proparian, as in *Madarocephalus*, which is always proparian, *Catillicephala*, in which some individuals are proparian, and *Distazeris*, which is at least close to the proparian state. (3) *Acheilus* has developed spinose pygidia closely similar to those found in such cheirurids as *Cheirurus*, *Cyrtometopus*, *Pseudosphaerexochus*, and *Actinopeltis*. (4) The acheilids have a bulbose frontal lobe on the glabella, a feature in which the resemblance to *Sphaerexochus* is especially prominent. (5) The principal development of *Acheilus* is in the Upper Cambrian, only a short stratigraphic distance below the first appearance of the Sphaerexochinae.

The inferred relationships between the Catillicephalinae and the Sphaerexochinae are shown in text-figure 4. The Catillicephalinae arose in late Middle Cambrian time, possibly as an off-shoot of the Corynexochinae. The smooth catillicephalid stock appeared early, before the beginning of the Upper Cambrian and continued into the Dresbachian, apparently dying out at or near the end of that stage.

The main acheilid stock gave rise in early Dresbachian time to two more offshoots, the somewhat effaced proparian *Madarocephalus*, and the furrowed, possibly proparian *Distazeris*.

It is impossible to say at present whether *Acheilus* or *Distazeris* represented the root stock in the early Dresbachian, for both genera have some specialized and some primitive features. It is certain, however, that *Acheilus* was the more vigorous of the two, for *Distazeris* is not known to range beyond the Dresbachian while *Acheilus* was abundant in Trempealeauian time and, as is here maintained, gave rise, by slight modification, to the early Ordovician Sphaerexochinae.

If this interpretation is correct, it will necessitate some changes in the higher taxonomy of the Cheiruracea, but that problem is beyond the scope of this article.

Genus ACHEILUS Clark, 1924

Denisia CLARK, 1924, not Hübner, 1825, Bull. Am. Paleontology, vol. 10, no. 41, p. 23.
Acheilus CLARK, June 1924, op. cit., p. 25.
Acheilus RAYMOND, July, 1924 (not Clark, June 1924) Boston Soc. Nat. History Proc., vol. 37, p. 422.
Acheilus (Raymond) KOBAYASHI, 1935, Imp. Univ. Tokyo Jour. Fac. Sci., sec. 2, vol. 4, pt. 2, p. 131.
Acheilus (Raymond) RASETTI, 1944, Jour. Paleontology, vol. 18, p. 235.
Denisia (Clark) RASETTI, op. cit., p. 241.
Theodenisia Clark, 1948, Jour. Paleontology, vol. 22, p. 643.

Genotype: *Acheilus levisensis* Clark, 1924, by monotypy.

The synonymy of this name is somewhat complicated because the genus, although first discovered by Raymond, was inadvertently published by Clark, in June, 1924, a month before Raymond's description appeared.

The first name used for the genus was *Denisia* Clark, but that name must be discarded as a homonym of *Denisia* Hübner, in Lepidoptera. Thus, the choice falls on *Acheilus* Clark, which is valid according to the Rules and takes precedence over *Acheilus* Raymond by prior publication. This fact has been overlooked, with the result that the genus, although legally based on *A. levisensis* Clark, 1924, by monotypy, has taken its form around *A. marcoui* Raymond, 1924, the type chosen by Raymond and a species far more typical of the genus than is *A. levisensis*.

The holotype of *A. levisensis* is a unique specimen, and it has been brushed with acid for cleaning so that some of the surface features are obscured, but close examination in reflected light shows that it does have the rectangular basal glabellar lobes and other structures of an *Acheilus*, as that genus has heretofore been understood. Thus the change in type very fortunately does not shift the generic concept.

However, there do seem to be two different types of *Acheilus*, which for the purposes of the discussion may be called the "*levisensis* type" and the "*marcoui* type."

TABLE 2.—CHARACTERISTICS OF THE CATILLICEPHALINAE

CATILLICEPHALINAE—Small corynexochids with tumid glabella and rectangular basal lobes

CATILLICEPHALID STOCK		ACHEILID STOCK				
General effacement; smooth pygidium		Furrows commonly well impressed; pygidium furrowed and spinose				
GENUS	*Catillicephala*	*Acheilus* (*A. levisensis* type)	*Acheilus* (*A. marcoui* type)	*Acheilus*, n. sp.	*Distazeris*	*Madarocephalus*
TYPE SPECIES	*Cephalocoelia ovoides* (=*Ucebia lata*) Raymond, 1937	*Acheilus levisensis* Clark, 1924		—	*Distazeris acuta* Raymond, 1937	*Madarocephalus olaetus* Resser, 1938
GLABELLAR SHAPE	Expanded anteriorly to subcircular, inflated	Slightly tapered	Parallel-sided or expanded anteriorly	Expanded anteriorly	Parallel-sided or expanded anteriorly	Expanded anteriorly
GLABELLAR FURROWS	Almost invariably absent	Present (1–2 pairs)	Commonly present (0–3 pairs)	1 pair	Present or absent	Rudimentary (2 pairs)
OCCIPITAL SPINE	Absent	Absent (node may be present)	Absent (node may be present)	Absent	Present	Present
DORSAL FURROWS	Impressed laterally, missing anteriorly	Effaced in front of glabella	Impressed laterally; missing anteriorly	Impressed all around	Impressed all around	Impressed laterally; missing anteriorly
POSITION OF EYES	Slightly behind midlength of glabella	At midlength of glabella	At midlength of glabella	At midlength of glabella	Anterior to midlength of glabella	Far forward
OCULAR RIDGE	Absent	?Present	Absent	Absent	Present	Absent
FACIAL SUTURES	Amphiparian	Opisthoparian	Opisthoparian	Proparian	?Proparian	Proparian
BRIM	Absent	Present	Absent	Present	Present	Absent

The features of both are outlined in Table 2, but fundamentally the difference is that the *levisensis* type has a frontal limb and the *marcoui* type does not.

I was at first tempted to recognize these two types as subgenera of *Acheilus*, but the discovery of the unique specimen described below as "*Acheilus* n. sp." shows that they are not sufficiently distinct even for that degree of taxonomic separation. *Acheilus* n. sp. has the brim of the *levisensis* type, but it has dorsal furrows well impressed in front of the glabella, a feature otherwise confined to the *marcoui* type. I thus agree with Rasetti (1944, p. 235), who also concluded that *Acheilus* should not be divided.

Rasetti (1944, p. 241) listed *Denisia* Clark as a valid genus but suggested that the presence of only one pair of glabellar furrows, the feature upon which Clark erected that genus, is not of generic value in a group that differs so much in this respect. *Denisia* and its replacement name, *Theodenisia*, are here suppressed as synonyms of *Acheilus*.

ACHEILUS n. sp.

A single cranidium of what appears to be a new *Acheilus* was found in Pebble 7 at the Rockledge Estate. It seems best to fit into *Acheilus*, but it differs from all other described species in the combination of a frontal limb, well-marked dorsal furrows in front of the glabella, and a typically acheilid glabellar shape. The nearest species is *A.? marginatus*, which has the first two features in common with this new species, but whose glabella is notably unlike other acheilids in shape. The species may be proparian.

This species is not named because better specimens are available in the collection from SA-EC-11, and it seems wiser to wait until that fauna can be described so that those specimens can be used as types.

Genus DISTAZERIS Raymond, 1937

Distazeris RAYMOND, 1937, Geol. Soc. America Bull., vol. 48, p. 1095.

Genotype: *Distazeris acuta* Raymond, 1937, by original designation.

Distazeris is known only from the cranidium, which in some respects resembles that of *Acheilus*. It differs in the advanced position of the eyes and in the presence of an occipital spine, which is unknown in *Acheilus*. The genus contains minute Catillicephalinae with glabella marked by catillicephalid glabellar furrows or effaced. A well-defined occipital ring extends backward into a horizontal spine. Dorsal furrows well impressed, either parallel or divergent anteriorly. Eyes set forward of the midlength of the glabella, if occipital ring is included in glabella. Ocular ridges present. Surface of test smooth or granulated. This genus may be proparian.

DISTAZERIS SIMPLEX (Raymond), 1937

Ucebia simplex RAYMOND, 1937, Geol. Soc. America Bull., vol. 48, p. 1103, pl. 2, fig. 5.

[Not] *Cephalocoelia? simplex* RASETTI, 1946, Jour. Paleontology, vol. 20, pp. 450–451, pl. 68, figs. 24–27 = *D? rasettii*, n. sp.

Diagnosis.—*Distazeris* with the glabella expanded anteriorly and lacking glabellar furrows.

Description.—Glabella smooth, sides diverging anteriorly. Occipital furrow shallow but clearly marked. Occipital ring with narrow horizontal spine extending from the posterior edge; junction of spine and occipital ring marked by slight declivity.

The frontal limb seems to have been broken from the holotype, as noted by Rasetti (1946, p. 450). Cheeks tumid, with low but clearly visible eyelines. Marginal furrows deep on posterior limbs. Palpebral lobes damaged on holotype, but eyes were short.

Measurements of the holotype (YPM 14724) with the occipital spine held horizontal are, in millimeters: sagittal intraoccipital length of glabella (B′), 1.3; sagittal length of occipital ring from middle of occipital furrow to juncture of occipital spine, 0.3; length of broken remnant of occipital spine, 0.3+; distance from middle of occipital furrow to eye-center, as projected on sagittal plane, 0.6; width of occipital ring (C), 1.1; width of glabella opposite center of eyes (M), 1.2; width of chord of posterior limb, 1.1; height of glabella above bottom of dorsal furrows, 0.5; estimated height of cranidium above tips of posterior limbs, 1.5; width of cranidium on center lines through eyes, measured on right side and doubled (E), 2.2.

Rasetti has identified several specimens from the Gaspé as belonging to this species, but they seem to differ sufficiently from the

holotype to warrant separation as a distinct species, which I here designate as *Distazeris? rasettii* Shaw, n. sp., with Laval University Nos. 1015a-c as syntypes. *D.? rasettii* differs from both *D. acuta* and *D. simplex* in having a granulated surface, from *D. acuta* in lacking glabellar furrows and in having the glabella expanded anteriorly.

COMMENTS ON THE SMOOTH TRILOBITES OF THE UPPER CAMBRIAN

The smooth Upper Cambrian trilobites have been much discussed and have been subjected to varying classifications. The Rockledge fauna includes some of them, and with this as a pretext, I have presumed to make an interim report on their classification.

The study of these trilobites began with the description of the genus *Plethopeltis* by Raymond (1913, p. 64), who assigned it to a new family, the Agraulidae.

The bulk of the genera were published in 1924 when Raymond described *Stenopilus* and assigned it, together with *Plethopeltis*, to the Ellipsocephalidae Matthew, 1887, Walcott described *Kingstonia*, *Bynumia*, and *Ucebia* without attempting to place them in any family, Clark described the smooth, eyeless *Leiocoryphe*, and Ulrich and Resser used the name *Camaraspis* for the first time.

After the sudden appearance of this large number of smooth genera Raymond (1925, p. 157) erected a new family, the Plethopeltidae, which he believe to have been derived from the Ellipsocephalidae, to include them all. Six years later Ulrich (in Bridge, 1931, pp. 219–222) put part of Raymond's *Plethopeltis* into a new genus, *Plethometopus*, but listed both under the heading "Family undetermined".

Next came the creation of the Tsinaniidae by Kobayashi (1933, p. 131) to include the smooth *Tsinania* Walcott, 1914, *Dictyella* Kobayashi, 1933, *Wongia* Sun, 1924, and *Dictya* Kobayashi, 1933. The last name was a homonym and was changed to *Dictyites* Kobayashi, 1936. In this family Kobayashi (1933, p. 142) included the Kingstoniinae, containing *Kingstonia*, *Bynumia*, and *Ucebia*.

Kobayashi (1935, p. 305) added *Giordanella* Bornemann, 1891, and *Maryvillia* Walcott, 1916, to the Tsinaniidae, at the same time shifting the Kingstoniinae to the Ellipsocephalidae (1935, pp. 201–203) and broadening the scope of the subfamily to include *Kingstonia*, *Ucebia*, *Bynumia*, *Plethopeltis*, *Stenopilus*, *Leiocoryphe*, *Plethometopus*, *Camaraspis*, *Wongia*, and *Triarthrella* Hall, 1863.

Resser (1936, p. 24, 1942, p. 51) next suppressed *Ucebia* as a synonym of *Kingstonia*.

In 1937, Raymond restricted the Tsinaniidae to *Tsinania*, *Dictyella*, and "*Dictya*" (Raymond, 1937, p. 1113); the Plethopeltidae he restricted to *Plethopeltis*, *Plethometopus*, and *Stenopilus* (op. cit., p. 1097). *Ucebia* was assigned to the Corynexochidae (op. cit., p. 1103), and *Bynumia* was not placed (op. cit., p. 1121).

Kobayashi (1938, p. 177) next reduced the Plethopeltidae to a subfamily of the Ellipsocephalidae and at the same time described a new genus, *Jubileia*, which he assigned to the Tsinaniidae (op. cit., p. 191). However, the flaring course of the anterior branches of the facial sutures seem to eliminate this genus from the family.

Lochman and Duncan (1944, p. 109) again raised the Plethopeltidae to a family and assigned to it the Kingstoniinae, including *Bynumia* and *Kingstonia*, thus reviving the Kingstoniinae of Kobayashi (1935); these authors also added *Ankoura* Resser, 1938, but their assigned cranidium seems ill-placed in either the Plethopeltidae or the Kingstoniinae.

Rasetti (1945, pp. 123–124) discussed the position of the *Stenopilus-Leiocoryphe-Plethometopus* group and concluded that the line is not related to *Bynumia* and *Kingstonia*. This confirms the opinions of Raymond (1937) and Kobayashi (1938) and denies Lochman and Duncan's (1944) grouping of the Plethopeltidae and the Kingstoniinae.

With this résumé as a background, we may now consider the present status of the classification of this group of trilobites, together with the position of the newly-defined genera *Arapahoia* Miller, 1936, *Hesperaspis* Stoyanow, 1936, *Ithycephalus* Resser, 1938, *Bynumina* Resser, 1942, and *Bynumiella* Resser, 1942. Although opinion is far from unanimous regarding these trilobites, certain generally entertained conclusions can be recognized: (1) *Plethometopus*,

Stenopilus and *Leiocoryphe* seem to form a closely-knit group that may at some time be separated from the plethopeltids but which is generally grouped with them in current taxonomy. (2) It seems to be agreed generally that they are not close relatives of the small-tailed plethopeltids except for Lochman and Duncan. (3) *Bynumia* and *Kingstonia* are related to each other and, the Tsinaniidae, as orginally established by Kobayashi (1933, p. 131), are recognized as a unit, but the subsequent additions are more or less disputed. (4) The Tsinaniidae are ancestral to the asaphids.

Combining these generalizations with the results of my own observations and the suggestions and criticisms of Dr. Rasetti the following provisional classification can now be made, both of the genera mentioned above and others to be discussed below;

Superfamily Ptychopariidea Richter, 1932
- Family Tsinaniidae Kobayashi, 1933
  - *Tsinania* Walcott, 1916
  - *Dictyella* Kobayashi, 1933
  - *Dictyites* Kobayashi, 1936
- Family Plethopeltidae Raymond, 1925
  - *Plethopeltis* Raymond, 1913
  - *Leiocoryphe* Clark, 1924
  - *Stenopilus* Raymond, 1924
  - *Camaraspis* Ulrich and Resser, 1924
  - *Plethometopus* Ulrich in Bridge, 1931
  - *Arapahoia* Miller, 1936 (synonym: *Hesperaspis* Stoyanow, 1936)
- Family Asaphiscidae Raymond, 1924
  - Subfamily Kingstoniinae Kobayashi, 1933
    - *Kingstonia* Walcott, 1924
      - (*Kingstonia*) s.s. (synonym: *Ithycephalus* Resser, 1938)
      - (*Ucebia*) Walcott, 1924
    - *Bynumia* Walcott, 1924
    - *Bynumina* Resser, 1942
    - *Bynumiella* Resser, 1942
  - Subfamily Asphiscinae Kobayashi, 1935 (synonym: Blountidae Lochman in Lochman and Duncan, 1944)
    - *Asaphiscus* Meek, 1873
    - *Blainia* Walcott, 1916
    - *Blountia* Walcott, 1916
      - (*Blountia*) s.s.
      - (*Homodictya*) Raymond, 1937
    - *Maryvillia* Walcott, 1916
    - *Protillaenus* Raymond, 1937 (synonym: *Blountiana* Lochman in Lochman and Duncan, 1944)

Suborder Ptychopariida Richter, 1932

Superfamily Ptychopariidea Richter, 1932

Family Tsinaniidae Kobayashi, 1935

Tsinanidae Kobayashi, 1935, Imp. Univ. Tokyo Jour. Fac. Sci., sec. 2, vol. 4, pt. 2, p. 305.

Kobayashi did not describe this group, but it includes derived asaphiscids with tapered, unfurrowed glabella, eyes placed behind the center of the cranidium and a many-segmented pygidium with narrow axial lobe and moderately well defined rim. Effacement is common on both shields. Facial sutures show the development of the median furrow of the asaphids.

In setting up the Tsinaniidae Kobayashi split off one group of species as the subfamily Kingston[i]inae, but this group is here referred to the Asaphiscidae. Likewise, *Maryvillia* is removed from the Tsinaniidae because of the lack of effacement and placed in the Asaphiscinae, although it appears that the Tsinaniidae arose from *Maryvillia*.

As here constituted, the Tsinaniidae include *Tsinania*, *Giordanella*, *Dictyella*, and *Dictyites*.

Family Plethopeltidae Raymond, 1925

Plethopeltidae Raymond, 1925, Vermont State Geologist 14th Rept. for 1923–24, p. 157.
Plethopeltidae Raymond, 1937, Geol. Soc. America Bull., vol. 48, p. 1097.
Plethopeltinae Kobayashi, 1938, Japanese Jour. Geology and Geography, vol. 15, nos. 3–4, p. 177 (placed in Ellipsocephalidae).
Plethopeltidae Lochman & Duncan, 1944, Geol. Soc. America Special Paper 54, p. 109.

Opisthoparia with small, subhemispheric cephalon: short, truncate glabella, commonly effaced; small eyes on steeply sloping cheeks. Pygidium small, without rim, transverse. Axial lobe well defined or effaced. The genera that are now commonly included are *Plethopeltis*, *Stenopilus*, *Leiocoryphe*, *Camaraspis*, and *Plethometopus*. To these I would add *Arapahoia* Miller, 1936, and its synonym (Resser, 1937, p. 2) *Hesperaspis* Stoyanow, 1936.

Genus Leiocoryphe Clark, 1924

Leiocoryphe? prisca Rasetti, 1946

Plate 57, figure 42

Leiocoryphe? prisca Rasetti, 1946, Jour. Paleontology, vol. 20, p. 457, pl. 70, fig. 5.

Three distorted cranidia have been found that appear in all respects to agree with Rasetti's figure.

The cranidium is entirely smooth, lacking all trace of furrows and of palpebral lobes. As in Rasetti's individual the anterior outline seems to have been semicircular, after allowance is made for distortion, and the doublure is probably absent. The posterior limbs are incomplete.

The species may be the one present in pebbles in the outcrop SA-EC-11 (Text-fig. 1).

The specimens are YPM 18627 from SA-EC-17 and MCZ 4429 and YPM 18628 from the matrix at SA-EC-16. A small fragment, possibly of this species was taken from Pebble 4 (YPM 18644).

Family ASAPHISCIDAE Raymond 1924

Asaphiscidae RAYMOND, 1924, Boston Soc. Nat. History Proc., vol. 37, p. 408.
Asphiscidae KOBAYASHI, 1935, Imp. Univ. Tokyo Jour. Fac. Sci., sec. 2, vol. 4, pt. 2, pp. 285–286, 290–291.

This family was erected by Raymond for *Asaphiscus*, *Blainia*, *Blountia*, and *Maryvillia*. Kobayashi placed *Maryvillia* in the Tsinaniidae, regarding it as did Walcott (1916B, p. 400) as the link between *Blainia* and *Tsinania*.

Maryvillia is here restored to the Asaphiscidae but this does not indicate any disagreement with Kobayashi or Walcott concerning the relations of *Blainia*, *Maryvillia*, and the Tsinaniidae.

Kobayashi added to the Asaphiscidae several other genera that are of no concern to us here and split the family into the Asaphiscinae and the Monkaspidinae to which I would add the Kingstoniinae, regarding them as derived blountiids.

Subfamily KINGSTONIINAE Kobayashi, 1933

Kingstoninae KOBAYASHI, 1933, Japanese Jour. Geology and Geography, vol. 11, nos. 1–2, p. 142.
Kingstoninae KOBAYASHI, 1935, Imp. Univ. Tokyo Jour. Fac. Sci., sec. 2, vol. 4, pt. 2, p. 201.
Kingstoninae LOCHMAN & DUNCAN, 1944, Geol. Soc. America Special Paper 54, p. 109.

Asaphiscidae in which the glabella, where visable on the interior of the cranidium, occupies nearly the full length of the cephalon. The facial sutures are transverse in the front so that an acute frontal limb is not developed as it is in the Tsinaniidae. Included genera: *Kingstonia* with its subgenera *Kingstonia* and *Ucebia*, *Bynumia*, *Bynumina*, and *Bynumiella*.

Genus KINGSTONIA Walcott, 1924
Subgenus KINGSTONIA Walcott, 1924

Kingstonia WALCOTT, 1924, Smithsonian Misc. Coll., vol. 75, no. 2, p. 58.
Kingstonia WALCOTT, 1925, op. cit., no. 3, p. 103.
Ithycephalus RESSER, 1938, Geol. Soc. America Special Paper 15, p. 82.

Genotype: *Kingstonia apion* Walcott, 1924.

Kingstonia, as it is now constituted, seems to contain two morphologic types. The first group, typified by the genotype, *K. apion*, has straight, parallel dorsal furrows (where they are visible), long, sharp-pointed, backswept, triangular posterior limbs, and in only a few species a narrow rim.

The other group is well shown in such species as *K. ara* (Walcott), 1924, *K. wal-*

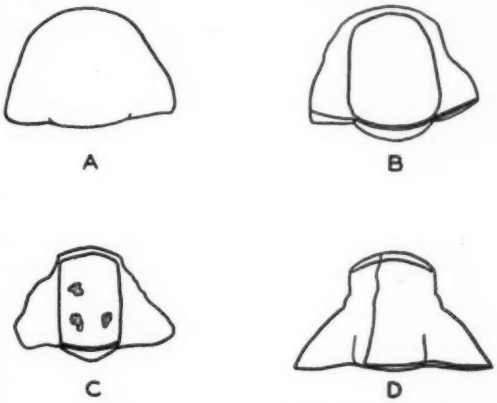

FIG. 5—The subgenera of *Kingstonia*. See text for explanation. A. Normal cranidium of *Kingstonia* (*Ucebia*) *vulgata* Resser, 1942. B. The same exfoliated. C. Holotype of *Ithycephalus typicalis* Resser, 1938. D. Holotype of *Kingstonia* (*Kingstonia*) *apion* Walcott, 1924. A and B after Resser, 1942. C after Resser, 1938. D after Walcott, 1925.

cotti and *K. inflata* Resser, 1938, *K. vulgata* Resser, 1942, and many others having an ovate cranidium, dorsal furrows that mark out a more or less rounded glabella, and stubby, rounded posterior limbs (text-fig. 5). A narrow rim in front of the cranidium is more common than in the first group. The shape of the effaced glabella and most of the other features seem to be somewhat intergrading, but the shape of the posterior limbs seems to differ consistently.

It happens that two names are now in the literature, which may conveniently be used in the subgeneric sense for these two groups. They are: *Kingstonia* (*Kingstonia*) for the species with the backswept, pointed posterior limbs (type of *K.* (*K.*) *apion*) and *Kingstonia* (*Ucebia*) for the more common

species with narrow, blunt posterior limbs (type of *K.* (*U.*) *ara*).

Ithycephalus was erected for an exfoliated cranidium called *I. typicalis* Resser, 1938, which seems in no way to differ from exfoliated specimens of *Kingstonia* (*Kingstonia*) (text-fig. 5C), so *Ithycephalus* is here suppressed.

KINGSTONIA (KINGSTONIA) SCRINIUM (Raymond), 1937
Plate 57, figures 46–48

Tsinania scrinium RAYMOND, 1937, Geol. Soc. America Bull., vol. 48, pp. 1113–1114, pl. 3, fig. 6.

This species was originally named from the tail, but a kingstoniid cranidium that seems to belong with it has been recovered.

Cranidium typical of *Kingstonia*, s.s., with wide triangular posterior limbs. Glabella poorly marked by dorsal furrows, even in exfoliated specimens. Cranidium strongly convex longitudinally. Occipital furrow poorly defined; occipital ring short. Frontal limb without rim but bearing irregular transverse striations (fig. 48). Eyes close to glabella; palpebral lobes short.

Pygidium elongate and smooth, with a poorly defined axial lobe extending full length of the shield. Margins turn abruptly downward. Partially exfoliated specimen (fig. 47) reveals poorly developed axial and pleural furrows.

The species is much like *K.* (*K.*) *gaspensis* Rasetti 1946, but the structure of the assigned pygidia separates the two.

Measurements from the unique cranidium found at SA-EC-16 (YPM 18626) are, in millimeters: Maximum length in sagittal plane (A), 5.8; width of occipital ring (C), 4.8; center line of eyes to rear of cranidium, projected into sagittal plane (D), 3.8; width of cranidium between centers of palpebral lobes (E), 6.8; length of palpebral lobes (P), 0.4.

Dimensions of a pygidium from Pebble A (MCZ 4959) in millimeters are: Maximum width (W), 7.3; anterior width of axial lobe (X), 2.9; length of axial lobe, including articulating half-ring (Y), 5.5; length of axial lobe, excluding half-ring (Y′), 4.7; length of pygidium, including half-ring (Z), 5.5. Four segments plus half-ring and terminal lobe visible on the specimen where exfoliated.

PYGIDIUM No. 5
Plate 57, figures 40, 41

This pygidium resembles the type of *Tsinania scrinium*, and the figured specimen was identified with that species by Raymond, but it differs in its unusually wide axial lobe.

Dimensions in millimeters from the unique specimen (MCZ 4985) from SA-EC-16 are: Maximum width, 6.6; anterior width of axial lobe, 3.3; length of axial lobe, including articulating half-ring, 4.4; length of pygidium, including half-ring, 4.4; no visible furrows; not exfoliated.

Genus BYNUMIA Walcott, 1924

Bynumia WALCOTT, 1924, Smithsonian Misc. Coll., vol. 75, no. 2, p. 54.
Bynumia WALCOTT, 1924, op. cit., no. 3, p. 17.
Bynumia RAYMOND, 1937, Geol. Soc. America Bull., vol. 48, p. 1121.
Bynumia LOCHMAN & DUNCAN, 1944, Geol. Soc. America Special Paper 54, pp. 111–112 (describe and illustrate the genotype).

Genotype: *Bynumia eumus* Walcott, 1924.

Effaced Kingstoniinae with a triangular cranidium. Glabella ovate, truncated, poorly defined. Frontal limb convex, commonly without rim. Assigned pygidia large, subtriangular, with narrow axial lobe; pleural and axial furrows present or effaced, depending upon species.

BYNUMIA LEPTOGASTER Raymond, 1937
Plate 57, figures 12, 13

Bynumia leptogaster RAYMOND, 1937, Geol. Soc. America Bull., vol. 48, pp. 1121–1122, pl. 3, figs. 19–20.

Raymond's description is adequate, but he failed to describe the low, convex rim that distinguishes this species from all others, nor is it well shown in the original figure. The presence of this rim, together with the somewhat better impressed dorsal furrows and the absence of a sharply pointed anterior cranidial outline all suggest that *B. leptogaster* is a primitive member of the genus.

Measurements in millimeters, with allowance made as nearly as possible for distortion, of a cast (Univ. Wyoming IT-70) of the holotype cranidium (YPM 14756) from Pebble 2, are: Front of cranidium to rear of glabella in sagittal plane (A), 9.0 (?); marginal furrow to rear of glabella, in sagittal plane (A′), 8.0; width of occipital ring

(C), 4.4; length of glabella (B), 7.0; center-line of eyes to rear of glabella, projected onto sagittal plane of head (D), 5.3 (?); width of cranidium across center-line of palpebral lobes (E), 3.6 (?); width of chord of posterior limb, 3.6; width of brim at intersection of marginal furrow and facial sutures (G), 5.2 (?); width of glabella on center-line of palpebral lobes (M), 3.6.

Measurements in millimeters of a cast (Univ. Wyoming IT-71) of the paratype pygidium (YPM 14757) from Pebble 2, and a small pygidium (MCZ 4962) from Pebble 1, provisionally assigned to the species, are as follows (dimensions italicized were obtained by measuring half of the specimen and doubling): Maximum width (W), *11.6*, 4.2; maximum width of axial lobe (X), *3.2*, 1.5; length of axial lobe (Y), 6.0, 2.6; length of pygidium (Z), 7.6, 2.8; no pleural ribs or axial rings visible on the larger specimen; two rings plus the half-ring and terminal lobe on smaller.

Subfamily ASAPHISCINAE Kobayashi, 1935

Asaphiscidae KOBAYASHI, 1935, Imp. Univ. Tokyo Jour. Fac. Sci., sec. 2, vol. 4, pt. 2, p. 293 (typographical error for Asaphiscinae).
Blountidae LOCHMAN in Lochman & Duncan, 1944, Geol. Soc. America Special Paper 54, p. 42.

Lochman's proposed family seems in no way to differ from the Asaphiscinae as defined by Kobayashi.

Genus BLOUNTIA Walcott, 1916
Subgenus HOMODICTYA Raymond, 1937

Homodictya RAYMOND, 1937, Geol. Soc. America Bull., vol. 48, p. 1114.
Homodictya RASETTI, 1946, Jour. Paleontology, vo.. 20, p. 454.

Genotype: *Homodictya imitatrix* Raymond, 1937 (=*Kaninia*? *platys* Raymond, 1937).

Homodictya was erected to receive a cranidium called *H. imitatrix*. The pygidium assigned by Raymond was removed by Rasetti, who substituted a *Blountia*-like tail. Before I became aware of Rasetti's action I had come to the same conclusion and regarded the pygidium chosen by him, which is also present in the Rockledge, as the one properly belonging to *H. imitatrix*. This pygidium has been named *Kaninia*? *platys* Raymond, 1937, which has page priority over *H. imitatrix*, but Article 28 of the Rules permits the first reviser to select any one of several names of equal age, and, therefore, because Rasetti has already discussed the species under the name "*H. imitatrix*", I shall suppress the trivial name "*platys*".

The close similarity of *Blountia* and *Homodictya* is manifest when the assigned pygidium is changed and the latter, it seems to me should be regarded as no more than a subgenus of *Blountia*, distinguished from the typical subgenus only by the effacement of the dorsal furrows.

Blountia cora Lochman in Lochman and Duncan, 1944, seems to be an *Homodictya*.

BLOUNTIA (HOMODICTYA) IMITATRIX (Raymond), 1937
Plate 57, figures 25–28

Kaninia? platys RAYMOND, 1937, Geol. Soc. America Bull., vol. 48, pp. 1110–1111, pl. 3, fig. 4.
Homodictya imitatrix RAYMOND, 1937 (part), op. cit., p. 1114, pl. 3, fig. 7 only. Fig. 8 (pygidium) assigned to *Coosella? minuta* (Raymond), 1937.
Coleopachys strix RAYMOND, 1937 (part), op. cit., p. 1120, pl. 3, fig. 15 only. Fig. 14 (cranidium) assigned to *Coosella? minuta*.
Homodictya imitatrix RASETTI, 1946, Jour. Paleontology, vol. 20, p. 454, pl. 69, figs. 8–13.

This species has been fully described by Rasetti on the basis of much better preserved specimens of both head and tail than those available from the Rockledge, and nothing further can be added at this time.

Dimensions in millimeters of the four available cranidia are given below. They are taken, respectively, from a cast (Univ. Wyoming IT-69) of the holotype (YPM 14745), and plesiotypes from SA-EC-16 (MCZ 4982), Pebble C at SA-SC-13P (MCZ 4988), and SA-EC-16 (MCZ 4967). Italicized dimensions were measured on one side and doubled.

Maximum cranidial length in sagittal plane (A), 3.5, 1.2, 5.4, 6.3; length of glabella, including occipital ring (B), 2.5, 0.95, 4.0, 4.1; length of glabella excluding ring (B′), ——, 0.85, 3.5, ——; center of eyes to rear of glabella, projected into sagittal plane (D), 1.9, 0.7, ——, 2.9; width of occipital ring (C), 1.9, 0.55, *2.6*, 2.8; width of cranidium across center points of eyes (E), *2.9*, 1.2, ——, 4.0; width of chord of posterior limb, 1.7, 0.7, ——, 2.5 (?); width of brim (G), 3.5, 1.1, *4.4*, 5.0; width of glabella opposite center of eyes (M), 1.9,

0.6, ——, 2.6; length of palpebral lobes (P), 0.6, 0.2, ——, 0.8.

The pygidia include a plesiotype from SA-EC-16 (MCZ 4968), another from Pebble C at SA-SC-13P (MCZ 4988), one from Pebble A at SA-EC-17P (MCZ 4958), a cast (Univ. Wyoming IT-55) of the paratype pygidium of *Coleopachys strix* (YPM 14752) from Pebble 2 at SA-EC-17P, and a cast (Univ. Wyoming IT-60) of the holotype of *Kaninia? platys* (YPM 14738) also from Pebble 2.

Maximum pygidial width (W), 3.5, 6.7, 8.2, 8.9, 12.0; maximum width of axial lobe, excluding articulating half-ring (X), 0.8, 2.2, 2.4, 2.6, 2.7; length of pygidium in sagittal plane, including half-ring (Z), 2.4, 4.1, 4.0, ——, 6.1; length of axial lobe, including half-ring (Y), 1.7, 3.4, 3.8, ——, 4.6; sagittal length of half-ring, ——, 0.15, 0.2, ——, 0.5.

Acrohybus argutus Raymond, 1937

Acrohybus argutus Raymond, 1937, Geol. Soc. America Bull., vol. 48, p. 1096, pl. 1, figs. 29.

This species was erected upon a single cranidium that apparently was placed in the collections of the Museum of Comparative Zoölogy. Unfortunately, I was not able to locate the type. However, the similarity of Raymond's description and figure of *A. argutus* to those of *Blountia* (*Homodictya*) *imitatrix* should be noted and the suggestion made that the two may be synonymous, but until the type is located *A. argutus* must be regarded as valid.

Genus Protillaenus Raymond, 1937

Protillaenus Raymond, 1937, Geol. Soc. America Bull., vol. 48, p. 1118.
Blountina Lochman in Lochman & Duncan, 1944, Geol. Soc. America Special Paper 54, pp. 55–56.

Genotype: *Protillaenus marginatus* Raymond, 1937, by original designation.

Lochman has listed the diagnostic features of *Blountina* as the obsolescence of the furrows, flattening of the profile of the cranidium, subquadrate shape of the glabella, and in the pygidium an obsolescence of the furrows, with all of these changes being a trend away from the typical structure of *Blountia*. *Protillaenus* agrees closely with them all, and for that reason the name *Blountina* is here suppressed as a junior synonym of *Protillaenus*.

There are some differences between the genotype of *Protillaenus*, *P. marginatus*, and the more typical forms of *Blountina*, but they may easily be accounted for by the fact that *P. marginatus* is older than most species now assigned to *Blountina* and hence represents an earlier stage in the development of the genus.

Protillaenus marginatus Raymond, 1937

Plate 57, figures 14, 15

Protillaenus marginatus Raymond, 1937, Geol. Soc. America Bull., vol. 48, p. 1118, pl. 3, fig. 10.

Cranidium smooth and convex. Fixed cheeks wide. Eyes small. Posterior limbs furrowed, but other furrows not well impressed. Flat rim deflected abruptly outward and of equal width all across front of cranidium.

A study of one of the two paratypes collected by Raymond (MCZ 4965) yields some additional information on the shape of the glabella, which is faintly, but completely, outlined. The glabella is sub-round but much wider than is typical of *Blountia*; it seems to be at an intermediate morphologic point between *Blountia* and the more typical *Blountina* structure. The occipital ring is narrow. Cheeks are narrowly confluent in front of the glabella. No certain trace of glabellar furrows.

The three known specimens are from Pebble 1 at the Rockledge estate. The holotype is MCZ 3827 and the paratypes are MCZ 4965. A cast of the figured specimen is IT-72 in the University of Wyoming collection.

Pygidium No. 3

Plate 57, figures 16, 17

Maryvillia triangularis Raymond, 1937, Geol. Soc. America Bull., vol. 48, p. 1112, pl. 3, fig. 3.
Blountia? triangularis Resser, 1942, Smithsonian Misc. Coll., vol. 101, p. 32.
[not] *Maryvillia triangularis* Raymond, 1924, Boston Soc. Nat. Hist. Proc., vol. 37, p. 410, pl. 12, fig. 21.
[not] *Maryvillia triangularis* Raymond, 1925, Vermont State Geol. 14th Rept. for 1923–1924, p. 155, pl. 12, fig. 21.

Maryvillia triangularis was first described in 1924 from two poorly preserved pygidia found in the Gorge formation at Highgate Falls. In 1937, Raymond described and figured under the same name another, bet-

ter-preserved pygidium collected from Pebble 2 at the Rockledge estate. An examination of the holotype reveals that it is too poorly preserved to permit certain identification, and a comparison with the specimens from the Rockledge shows differences that are clearly visible in Raymond's own figures. It thus appears that the Rockledge specimens cannot be referred to the Gorge species, which is based on YPM 4707.

The similarity of the Rockledge pygidium to that of *Blountina triangularis* Lochman (in Lochman and Duncan, 1944, pl. 8, figs. 12, 13, 15, 18) leads me to assign it to *Protillaenus marginatus*. The use of the trivial name "*triangularis*" by Raymond will not, of course, affect Lochman's specific name, because "*triangularis*" must be confined to Raymond's Gorge species.

Measurements in millimeters of the pygidium found in Pebble A at SA-SC-13P (MCZ 4989) are: maximum width (W), 8.5; maximum width of axial lobe, excluding articulating half-ring (X), 2.2; length of pygidium in sagittal plane, including half-ring (Z), 6.6; length of axial lobe, including half-ring (Y), 4.5; length of articulating half-ring in sagittal plane, 0.3; rings on axial lobe, excluding articulating ring and terminal segments, 7; visible pleural segments, 5.

Family CREPICEPHALIDAE Kobayashi, 1935

Crepicephalidae KOBAYASHI, 1935, Imp. Univ. Tokyo Jour. Fac. Sci., sec. 2, vol. 4, pt. 2, pp. 275–280.

Crepicephalidae LOCHMAN, 1936, Jour. Paleontology, vol. 10, p. 36.

The reference of *Meteoraspis* to the Crepicephalidae is made with some hesitation, for there are differences between *Meteoraspis* and the typical crepicephalids, but the shape of the glabella, of the entire pygidium, and of the eyes seems to relate the genus to this family.

Genus METEORASPIS Resser, 1935 (?)

Meteoraspis RESSER, 1935, Smithsonian Misc. Coll., vol. 93, no. 5, pp. 40–41.

Greylockia RAYMOND, 1937, Geol. Soc. America Bull., vol. 48, p. 1108.

Homodictya RAYMOND, 1937 (part), op. cit., p. 1114.

Coleopachys RAYMOND, 1937 (part), op. cit., p. 1120.

Genotype: *Ptychoparia? metra* Walcott, 1891, by original designation.

As is discussed below, *Greylockia* Raymond and *Coleopachys* Raymond seem to fall into synonymy with *Meteoraspis*.

METEORASPIS? MINUTA (Raymond), 1937

Plate 57, figures 8–10

Greylockia minuta RAYMOND, 1937, Geol. Soc. America Bull., vol. 48, pp. 1108–1109, pl. 2, fig. 16.

Dunderbergia vermontensis RAYMOND, 1937, op. cit., p. 1112, pl. 3, fig. 9.

Coleopachys strix RAYMOND, 1937 (part), op. cit., p. 1120, pl. 3, fig. 14 only (cranidium). Fig. 15 (pygidium) assigned to *Blountia* (*Homodictya*) *imitatrix*.

Coleopachys pisum RAYMOND, 1937, op. cit., p. 1120, pl. 3, fig. 16.

Raymond appears to have split one species into several separately-named groups, namely, *Greylockia minuta*, *Coleopachys strix*, *C. pisum*, and *Dunderbergia vermontensis*.

A graphical comparison has been made of all available specimens of these "species", including the types of each. In all cases the similarity is so close that statistical treatment is not needed to demonstrate that no significant differences exist among them. The raw data are included below.

All of the differences that have been used to separate the above-named "species" can be explained as due to ontogenetic changes or to preservation. Thus, *Coleopachys pisum* and *Dunderbergia vermontensis* are young individuals, *Greylockia minuta* is based on cranidia of intermediate size, and *C. strix* was used for large cranidia from which the rim had been broken.

Raymond regarded the absence of the rim as the generic feature of *Coleopachys*, although he recognized that *Coleopachys* was closely similar to *Greylockia* when he stated (Raymond, 1937, p. 1109):

"*Greylockia minuta* more closely resembles the associated *Coleopachys strix* than it does any of the trilobites to which it is really related. If the rim were broken from a specimen of the former, it would be difficult to decide to which genus it should be referred."

Close scrutiny of the types of *C. strix* show that most of them do retain parts of a rim, indicating that its absence is due to poor preservation and is not an original feature of the cranidium.

If all four names are thus synonymous,

G. minuta should probably be taken in preference to the others because it is based on the most complete, adult specimens. Thus, *Coleopachys* is suppressed in favor of *Greylockia*, and *Greylockia*, in turn, is suppressed in favor of *Meteoraspis*.

Undistorted mature cranidia of *Meteoraspis? minuta* have an ovate glabella, rounded in front. Glabella in younger cranidia is relatively shorter, giving it a stubbier appearance. Glabella convex in both directions, smooth save for the well-marked occipital furrow. Dorsal furrows deep.

Fixed cheeks are smooth, narrow and confluent in front in a narrow convex brim. Eyes prominent; palpebral furrow well marked.

The facial sutures come straight backward and slightly outward from the front of the head to the eyes. From the rear of the palpebral lobes the sutures turn directly outward, then backward, to form a rectangular rather than a triangular posterior limb (fig. 8). The marginal furrow is not a continuation of the occipital furrow.

The pygidium assigned by Raymond to *Coleopachys strix* is now placed with *Blountia* (*Homodictya*) *imitatrix* (Raymond), 1937.

The measured cranidia include, respectively, U. Wyo. IT-56 from Pebble 5, the holotype of *Coleopachys pisum* (YPM 14750) from SA-EC-16, the holotype of *Dunderbergia vermontensis* (YPM 14742) from SA-EC-16, the holotype of *Greylockia minuta* (YPM 14734) from Pebble 2, MCZ 4969 from SA-EC-6, cast of an unnumbered paratype of *Coleopachys strix* (U. Wyo. IT-54) in the Yale collections from SA-EC-16, and the holotype of *C. strix* (YPM 14751) from Pebble 2.

Measurements are in millimeters, with italicized dimensions representing measurements taken on one-half of damaged specimens and doubled. The letters in parentheses refer to the dimensions shown in text-figure 2. Total cranidial length (A), 2.7, ——, ——, ——, 7.9, ——, ——; length of head between marginal furrow and rear of occipital ring in sagittal plane (A′), 2.4, 2.4, ——, 3.2?, 6.7, 7.5, ——; length of glabella, including occipital ring (B), 2.1, 2.1, 2.7, 2.8, 6.0, 7.1, 9.4; length of glabella, excluding occipital ring (B′), 1.6, 1.6, 2.0, 2.3, 4.8, 5.5, 7.7; width of occipital lobe (C), 1.6, 1.8, *2.1*, 2.1, 4.9, 5.6, 7.5; distance from center of palpebral lobes to rear of occipital lobe, projected onto sagittal plane (D), ——, 1.2?, 1.8, 1.7, 3.9, 3.9, 5.5; width of cranidium between centers of palpebral lobes (E), ——, ——, 3.2, 3.2, 7.2?, *9.2*, 12.5; width of glabella opposite centers of palpebral lobes (M), ——, 1.5, 1.8, 1.9, 4.3, 5.5, 6.9.

PYGIDIUM No. 6
Plate 57, figure 11

Paracrepicephalus cf. *P. thoosa* (Walcott) RAYMOND, 1937, Geol. Soc. America Bull., vol. 48, p. 1097, pl. 3, fig. 25.

A single, incomplete pygidium, from which the spines had been broken (YPM 14714) was described and figured by Raymond. During the re-examination of the type material at the MCZ the counterpart (MCZ 4985) of this specimen from SA-EC-16 was discovered. It retains more of the spines than does the original so a rubber squeeze (Univ. Wyoming IT-63) of it is figured. This pygidium is tentatively associated with *Meteoraspis? minuta*.

PYGIDIUM No. 2
Plate 57, figures 31, 32

Undetermined Trilobite Pygidium RASETTI, 1946, Jour. Paleontology, vol. 20, p. 462, pl. 69, figs. 14, 15.

Rasetti has figured but declined to name an unusual pygidium which cannot now be matched with any cranidium. I fully agree with him that it is not wise to erect new names for pygidia alone, so I have simply designated the specimen by number. The figured specimen (YPM 18461) was taken from SA-EC-17 and is smaller than Rasetti's, but it agrees in all respects with the figured type.

I have placed it provisionally with the Crepicephalidae because of the similarity to the normal crepicephalid pygidium, save for the absence of the pair of long spines.

Family PTYCHOPARIIDAE Matthew, 1888
Subfamily MENOMONIINAE Walcott, 1916, emended

Menomonidae WALCOTT, 1916, Smithsonian Misc. Coll., vol. 64, no. 3, p. 161.
Nepeidae WHITEHOUSE, 1939, Queensland Mus. Mem., vol. 11, pt. 3, p. 210.
Menomonidae LOCHMAN & DUNCAN, 1944, Geol. Soc. America Special Paper 54, p. 133.

Minute trilobites characterized by extremely long thoraces. Cranidium bears small conical glabella. Frontal limb with upturned rim enclosing steeply inclined concave brim. Brim develops a median boss in the adult of some species. Cranidium narrow between palpebral lobes. Eyes small in all genera and, in most, mounted atop inflated globose cheeks; eyes stalked in some species. Posterior limbs characteristically strap-like, with posterior branch of facial suture either opisthoparian or proparian. Free cheeks gibbose, confluent in front of the cranidium, and in most genera, smooth; free cheeks appear to be separated by a median suture in all genera save *Dresbachia*.

Thorax very long, ranging up to 42 segments in *Menomonia calymenoides* (Whitfield), 1878. Axial lobe occupies about one-third of the thoracic width. In all genera for which the thorax is known, the pleural furrows occupy a median position and run straight out to the ends of the segments rather than diagonally across them. Pygidium extremely minute.

There are now recognized in Middle and Upper Cambrian rocks a number of small trilobites that fit this general characterization. They have been included in the families Menomoniidae and Nepeidae depending upon whether they are proparian or opisthoparian, respectively.

As has been indicated above in the discussion of the Catillicephalinae, the proparian condition seems to be progressive, appearing in terminal members of many lines, and is, therefore, of little importance in separating higher taxonomic categories. This is not a new discovery but simply a reaffirmation of a point made by critics of the Beecher classification.

If it be granted that the course of the posterior branch of the facial sutures is not of superlative importance in the classification of the trilobites, there seems to be little reason for recognizing two separate groups for these small forms, and, consequently, the name Nepeidae may be suppressed as synonymous with Menomoniinae. The following genera seem to belong here: *Menomonia* Walcott 1916, *Millardia* Walcott 1916, not Thomas 1911, *Bolaspis* Resser 1935, *Bolaspidella* Resser 1937, and *Nepea* Whitehouse 1939. *Dresbachia* Walcott 1916, may be included provisionally, as can *Knechtelia* Lochman 1950, although both of these genera differ from the typical genera in some important respects. *Acrocephalops* Poulsen, 1927, which Whitehouse included in the Nepeidae, has pleural furrows on the thorax that are different from those of the typical Menomoniinae.

Alokistocare Lorenz 1906 was included in the Nepeidae by Whitehouse but was made the type of a separate family, the Alokistocaridae, by Resser in 1937. *Alokistocare* does not belong in the emended Menomoniinae, and it seems probable that the family Alokistocaridae will stand.

Deiracephalus Resser 1935 bears a superficial resemblance to some members of the Menomoniinae because of the median ridge developed on the frontal limb, but it differs fundamentally in the depressed structure of the fixed cheeks and in the excessive width of the frontal limb.

Lochman and Duncan have assigned *Bridgeia* Lochman 1944 to the family, but the absence of strap-like posterior limbs, the position of the eyes below the summit of the cheeks, the parallel-sided glabella, and other structures seem to eliminate it from association with the genera listed above.

Genus DENSONELLA Shaw, new name

Millardia WALCOTT, 1916, not Thomas, 1911, Smithsonian Misc. Coll., vol. 64, no. 3, p. 163.
Menomonia RESSER, 1938 (part), Smithsonian Misc. Coll., vol. 97, no. 10, pp. 34–35.
Millardia LOCHMAN, 1940, Jour. Paleontology, vol. 14, pp. 9–10.

It has been overlooked that *Millardia* Walcott 1916 is an homonym of *Millardia* Thomas 1911, in Mammalia, and was thus unavailable to Walcott for a trilobite. The new name *Densonella* is here proposed to replace it, with *Millardia semele* Walcott 1916 as the genotype.

Genus BOLASPIDELLA Resser, 1937

Bolaspidella RESSER, 1937, Smithsonian Misc. Coll., vol. 95, no. 22, p. 3.
Hysteropleura RAYMOND, 1937, Geol. Soc. America Bull., vol. 48, p. 1094.

Genotype: *Ptychoparia housensis* Walcott, 1886.

Raymond diagnosed *Hysteropleura* thus: "Solenopleuridae similar to *Bolaspis* Resser, but without a boss in front of the glabella."

A complete discussion of the validity of the genus *Hysteropleura* will be given in a subsequent paper on the Skeels Corners formation, but it should be noted that an examination of the types involved leads me to believe that *Bolaspidella*, *Hysteropleura*, and *Apedopyanus* Raymond, 1937, are synonymous.

BOLASPIDELLA MACGERRIGLEI
(Raymond), 1937
Plate 57, figure 44

Hysteropleura macgerriglei RAYMOND, 1937, Geol. Soc. America Bull., vol. 48, p. 1094, pl. 1, fig. 22.

Species known only from cranidia, which are small and possibly immature, rarely exceeding 3 mm. in length. Glabella subconical, truncate anteriorly. Occipital furrow deeply impressed, setting off occipital ring bearing wide, triangular occipital spine. Fixed cheeks prominent, rising higher than the glabella opposite the eyes. Palpebral lobes small, eyes apparently set on short stalks. Brim slightly convex, but set off in front by an abruptly upturned rim, on the sides by steeply sloping cheeks, and in the rear by the sharply rising front of the glabella, so that it appears to be concave. This species might in many ways be called an opisthoparian "*Millardia*".

Measurements in millimeters of the figured paratype (MCZ 4984) from SA-EC-16 are: Anterior cranidial margin to rear of damaged occipital spine, 3.4?; anterior cranidial margin to occipital furrow, on center line (A′), 2.3; anterior end of glabella to rear of occipital spine, 2.5?; anterior end of glabella to occipital furrow, on center line (B′), 1.4; width of occipital ring (C), 1.4; center line of palpebral lobes to occipital furrow, projected onto center line (D), 1.3; width of cranidium between centers of palpebral lobes, measured on right side and doubled (E), 3.2; width of brim between intersections of facial sutures and marginal furrow (G), 1.3; width of glabella opposite midpoints of palpebral lobes (M), 0.7; length of palpebral lobes (P), 0.2.

Subfamily PTEROCEPHALIINAE
Kobayashi, 1935

Pterocephalinae KOBYASHI, 1935, Imp. Univ. Tokyo Jour. Fac. Sci., sec. 2, vol. 4, pt. 2, pp. 230–231.

Genus COOSIA Walcott, 1911 (?)
COOSIA? sp.
Plate 57, figures 35–37

Eight incomplete cranidia of what appear to be a species of *Coosia* have been found in the matrix at SA-EC-16, but they are not sufficiently well preserved to serve as a basis for the erection of a new species or even to provide an unequivocal generic identification.

The glabella is elongate-conical and appears to be smooth, except for the occipital furrow, which is well impressed, but shallower medially than at the sides. Dorsal and marginal furrows are well impressed. The frontal limb comprises a broad, flat, upturned rim and a flat, downsloping brim of about equal length. The largest cranidium (MCZ 4980) shows a median shallowing of the marginal furrow, suggesting an incipient median boss, but this structure may be due to preservation.

The fixed cheeks are narrow and markedly upsloping, capped by long palpebral lobes. There are no ocular ridges. The facial sutures run straight forward in front of the eyes and straight out to the sides, behind.

The surface is smooth, and the shell material appears to have irregularly disposed puncta scattered over it.

Compared with *Meteoraspis*? *minuta*, which this species most closely resembles, *Coosia*? sp. has a relatively narrower glabella, notably narrower and more elevated fixed cheeks, and a flat rather than a convex rim.

Eight cranidia have been measured, they are MCZ 4981 from SA-EC-16; MCZ 4959 from Pebble A at SA-EC-16; MCZ 4966, U. Wyo. IT-57, MCZ 4980 from SA-EC-16; and three paratypes of *Coleopachys strix* (MCZ 4458, 4976, 4975) from SA-EC-16.

Dimensions are in millimeters and those given in italics have been measured on one side of damaged specimens and doubled. The letters in parentheses refer to text-figure 2. Total cranidial length (A), 3.4, 4.3, 4.5, ——, 6.0, ——, ——, ——; cranidial length from marginal furrow to rear of occipital lobe (A′), 3.0, 3.7, 3.8, ——, 5.2, 7.0, 9.0, ——; glabellar length, including occipital lobe (B), 2.6, 3.1, 3.2, ——, 4.5,

6.2, 8.3, ——; glabellar length, excluding occipital lobe (B′), 2.0, 2.7, 2.6, 3.0, 3.9, 5.0, 6.5, 9.4; width of occipital ring (C), 1.8, 2.5, *2.4*, ——, 2.6, ——, *5.0*, ——; distance from center of palpebral lobes to rear of occipital lobe, projected onto sagittal plane (D), 1.5, 1.7?, 2.1?, ——, 2.8, ——, 5.2, ——; width of cranidium between centers of palpebral lobes (E), *3.8*, ——, ——, ——, ——, ——, 8.2, ——; width of chord of posterior limb, ——, ——, ——, ——, 2.3, ——, ——, ——; width of brim (G), ——, 3.0, *3.0*, *3.4*, 3.7, ——, ——, ——; width of glabella opposite center of palpebral lobes (M), 1.9, 2.1, 2.0, 2.4, 2.7, ——, 5.1, 7.8; length of palpebral lobes (P), ——, ——, ——, ——, 1.8, ——, ——, ——.

PYGIDIUM No. 4
Plate 57, figure 38

Homodictya imitatrix RAYMOND, 1937 (part), Geol. Soc. America Bull., vol. 48, p. 1114, pl. 3, fig. 8 only. Fig. 7 (cranidium) assigned to *Blountia* (*Homodictya*) *imitatrix*.

Rasetti (1946, p. 454) first removed this pygidium from *Homodictya imitatrix*, but he did not reassign it. It is here provisionally associated with the cranidium of *Coosia*? sp.

The pygidium is small, incomplete, and is represented by only one specimen (YPM 14746) from Pebble 2, but enough of it is preserved to suggest the assignment to *Coosia*?. One anterior groove is complete across the rhachis and a second pair is faintly developed laterally, but otherwise the lobe is unmarked. The pleural lobes are tumid and marked by two pairs of well-impressed interpleural grooves and faint traces of a third pair. The rim is wide, smooth, concave, and marked off from the rest of the shield by an abrupt change in slope. The rear margin is nearly straight. Measurements in millimeters of a cast (Univ. Wyoming IT-68) of the pygidium are: maximum width, measured on left side and doubled (W), *6.4;* anterior width of axial lobe (X), 1.6; length of axial lobe, including articulating half-ring (Y), 3.4; length of articulating half-ring, 0.3; length of pygidium, including half-ring (Z), 4.5.

This provisional association of head and tail may be incorrect because there is such a disparity in numbers of specimens (Table 1) and because Pebble 2, from which this pygidium was obtained, yielded no specimens of the head.

Family SOLENOPLEURIDAE Angelin, 1851
Subfamily SOLENOPLEURINAE
Kobayashi, 1935
Genus WELLERASPIS Kobayashi, 1935

Welleraspis KOBAYASHI, 1935, Imp. Univ. Tokyo Jour. Fac. Sci., sec. 2, vol. 4, pt. 2, pp. 263–264.
Welleraspis LOCHMAN, 1938, Jour. Paleontology, vol. 12, p. 469.
Welleraspis HOWELL, 1945, Geol. Soc. America Mem. 12, p. 2.

Genotype: *Liostracus? jerseyensis* Weller, 1900, by original designation.

Small solenopleurids with an oblong glabella, rounded in front, occupying most of the cranidium. Fixed cheeks narrow, slightly tumid, bearing eyes at about midlength of cranidium. Frontal limb short; cheeks narrowly confluent across brim; marginal furrow deep, setting off a prominent rim. Posterior limbs narrow, marked by deep furrow.

Pygidium small, transverse, with conical axial lobe extending to the marginal furrow in the rear. Both axial and pleural lobes furrowed. Rim narrow.

WELLERASPIS sp.
Plate 57, figures 18–20

Four fragmentary cranidia and three pygidia, described below as Pygidium No. 1, seem to belong to a new species of *Welleraspis*. The specimens agree in all respects with the characterization of the genus given above, but because of their poor preservation none of them would make a satisfactory type, and I refrain from introducing a new trivial name.

The glabella is a rounded oblong in the larger specimens but slightly tapered anteriorly in the smaller. Two or three pairs of glabellar furrows are present, and the posterior pair is deflected backward in a rectangular course reminiscent of that found in the Catillicephalinae. The occipital furrow is well impressed but shallow medially and it cuts off a bluntly triangular occipital spine. The ocular ridge is low and faint and runs to a long and narrow palpebral lobe. (fig. 19)

The posterior limbs are faintly granulated in one specimen, but the glabella is smooth in all of them.

The most immediately noticeable difference between this species, *W. jerseyensis*, and *W. newfoundlandensis* Lochman, 1938, is the presence in the last two of an occipital spine, but I agree with Lochman (1947, pp. 60–61) in questioning whether spines are actually of specific value.

The cranidia measured are MCZ 4972, 4970, 4971, and 4973, respectively. Italicized dimensions were measured on one side of the head and doubled. The letters in parentheses refer to text-figure 2. All measurements in millimeters.

Length of cranidium (A), ——, ——, 5.2, ——; length of cranidium from marginal furrow to rear of occipital ring (A′), ——, ——, 4.0, 4.8; glabellar length, including occipital ring (B), 2.4, 2.6, 4.6, ——; same, excluding occipital ring (B′), 1.9, 2.1, 3.6, 4.1; width of occipital ring (C), *1.6*, 1.6, 2.7, ——; distance from center of palpebral lobe to rear of occipital lobe, projected onto sagittal plane, 1.7, 1.9, 2.8, ——; distance from center of palpebral lobes to intersection of occipital and dorsal furrow (D′), 1.3, 1.2, 1.6, 2.3; width of cranidium across centers of palpebral lobes (E), *2.8, 3.0, 5.4, 6.6;* width of chord of posterior; limb, 1.2, ——, ——, ——; width of brim at intersection of facial sutures and marginal furrow (G), *2.2*, 2.5, *3.4, 5.6;* width of glabella opposite centers of palpebral lobes (M), *1.5*, 1.7, 3.2, *4.0;* length of palpebral lobes (P), ——, 0.8, ——, 1.4; pairs of glabellar furrows, 2, 3, 3, 3.

PYGIDIUM No. 1
Plate 57, figure 21

Three small pygidia that seem to belong to *Welleraspis* have been recovered from the basal sandy limestones at SA-EC-16, in association with the cranidia just described. They are transverse, with a conical axial lobe. The largest specimen shows three axial furrows and three interpleural grooves. The rim is well marked, set off by a marginal furrow, and is somewhat wider than that of the pygidium assigned to *W. jerseyensis*.

Measurements in millimeters of the pygidia, which are YPM 18643, MCZ 4974, and MCZ 4973, respectively, are given below. Italicized dimensions were found by measuring half of the specimen and doubling.

Maximum width (W), *4.6*, 5.0, 5.5; maximum width of axial lobe (excluding articulating half-ring) (X), *1.7*, 1.8, 2.0; length of axial lobe, including articulating half-ring (Y), ——, 2.0, 2.9; length of pygidium, including half-ring (Z), ——, 2.1(?), ——; length of axial lobe, excluding half-ring (Y′), 2.1, ——, 2.8; length of pygidium, excluding half-ring (Z′), 2.1, 1.9(?), ——.

PTYCHOPARIIDS OF UNCERTAIN POSITION
STENELYMUS KOBAYASHII Raymond, 1937
Plate 57, figures 33, 34

Stenelymus kobayashii RAYMOND, 1937, Geol. Soc. America Bull., vol. 48, pp. 1100–1101, pl. 2, fig. 1.

There is nothing to add to the original description. This small species is rare, and is known only from the holotype from Pebble 2 at SA-EC-17P.

Measurements in millimeters of a cast (Univ. Wyoming IT-59) of the holotype cranidium (YPM 14717) are: front of cranidium to occipital furrow in sagittal plane, 4.8; marginal furrow to occipital furrow on sagittal line, 4.1; front of glabella to occipital furrow (B′), 4.1; center of palpebral lobes to occipital furrow, projected onto sagittal plane, 2.0; width of cranidium at center line of palpebral lobes, measured on left side and doubled (E), 4.8; width of glabella on center line of palpebral lobes (M), 1.3; width of brim at intersection of facial sutures and marginal furrow (G), 3.9; width of chord of posterior limb, 2.1(?).

A minute cranidium (MCZ 4955) assigned to *?S. kobayashii* was found in Pebble A at SA-EC-17P.

"IDAHOIA" MINOR Raymond, 1937
Plate 57, figure 43

Idahoia minor RAYMOND, 1937, Geol. Soc. America Bull., vol. 48, p. 1113, pl. 3, fig. 5.

A small, imperfect cranidium was described and figured under this name by Raymond. The holotype was collected from the basal sandy limestone at SA-EC-16. The glabella is smooth, tapering rapidly forward and truncate in front. The frontal limb is narrow, with the brim being somewhat narrower than the prominent, convex rim; there is a deep marginal furrow. The occipital ring is narrower than the rear of the glabella, and is marked by a median node. Both fixed cheeks are damaged. The

posterior limbs are as wide as the glabella, but their forward parts are missing.

This specimen cannot now be placed in any genus because of its incomplete condition, although it does resemble certain species of *Blountia*. It is almost certainly not assignable to *Idahoia*.

Measurements in millimeters of a cast (Univ. Wyoming IT-58) of the holotype (YPM 14743) are: Length of frontal limb in sagittal plane, 1.1, comprising rim, 0.6 and brim, 0.5; length of glabella excluding occipital ring (B′), 2.4; width of occipital ring (C), 2.0; width of chord of posterior limb, 1.9.

FREE CHEEK No. 1
Plate 57, figure 39

A single large free cheek (MCZ 4952) has been taken from Pebble A at SA-EC-17P. It is figured because it is the largest fossil thus far found in the Rockledge conglomerate. It measures 25.2 mm. from the anterior angle to the tip of the genal spine.

Because its size far surpasses any of the cranidia collected, it cannot now be assigned with confidence to any described species, although the course of the facial sutures and the elevated eye suggest that it might belong either to *Meteoraspis? minuta* or to *Coosia?* sp.

Order AGNOSTIDA Kobayashi, 1935
Superfamily AGNOSTIDEA Salter, 1864
Family AGNOSTIDAE M'Coy, 1849
Subfamily AGNOSTINAE Raymond, 1913
Genus ACMARHACHIS Resser, 1938

Acmarhachis Resser, 1938, Geol. Soc. America Special Paper 15, p. 47.

ACMARHACHIS sp. indet.
Plate 57, figures 22–24

Two cephala and two pygidia referable to this genus were recovered from the matrix of the conglomerate at SA-EC-16. One tail (Figs. 23, 24) was broken from the holotype of *Distazeris? simplex* during its examination. One head (MCZ 4978) was labelled by Raymond as "*Agnostus innocens* Clark," although it was not described or figured.

The tail is clearly assignable to the genus, and the cephalon, although of a type common to the Agnostinae, is much like that of *A. typicalis* Resser, 1938, the genotype, but the two specimens available of each shield are neither sufficient material to prove that the species is *A. typicalis* nor are they enough to serve as basis for a new species, if it is not *A. typicalis*.

The outline of the axial lobe of the pygidium is typical of the genus. The rim is nearly flat, inclined downward, and well marked all around. There is a small pair of posterolateral spines.

The cephalon has a glabella that is cut by two sets of transverse furrows; the anterior furrow is complete across the glabella, the posterior, obsolete mesially; the posterior part of the glabella stands higher than the anterior segments and is surmounted by a small, low median node. Small triangular basal glabellar lobes are present. The surface of the cheeks is smooth, and there is no median preglabellar furrow. The rim, where preserved, is well marked, but narrower than the pygidial rim. There do not appear to have been any genal spines, but the poor preservation of the genal angles makes it impossible to be truly certain of their absence.

Measurements in millimeters of two cephala (MCZ 4978 and 4990) are: Front of glabella to rear, 2.3, 1.55; width across outer extremities of basal glabellar lobes, 1.9, 1.2; maximum width of anterior glabellar lobe, 1.4, 0.8; marginal furrow to rear of glabella in sagittal plane, 2.7, 2.0; maximum width of cephalon between marginal furrows, 3.6, 2.3(?); rear of glabella to anterior glabellar furrow, 1.5, 1.1; rear of glabella to posterior glabellar furrow, 1.1, 0.8. MCZ 4978 has been squeezed from front to rear, widening the cephalon laterally.

Measurements in millimeters of the pygidia (MCZ 4977 and YPM 18647) as nearly as they can be determined after allowance has been made in the former for distortion are: Total length in sagittal plane, 3.3, 2.1; anterior edge to marginal furrow at posterior end of axial lobe, 3.0, 1.8; anterior edge to second transverse furrow across axial lobe, in sagittal plane, 1.0, 0.7; anterior edge to first transverse furrow, 0.5, 0.3; maximum width of anterior lobe of rhachis, 1.9, 0.9; maximum width of posterior lobe, 2.0, 1.0; maximum width of shield between lateral marginal furrows, 3.6, 1.8; maximum width of shield between outer margins, 4.1, 2.1.

AGNOSTID No. 1
Plate 57, figures 29, 30

Another agnostid cephalon has been found in the basal sandy limestone at SA-EC-16 (MCZ 4983) and in Pebble A (MCZ 4957) at SA-EC-17P. Both are poorly preserved and cannot be identified generically, but they seem to belong to a single species.

Measurements in millimeters on MCZ 4957 and MCZ 4983 respectively, are: Total length in sagittal plane, 3.9, ——; total glabellar length, 2.8, 2.8; width across outer ends of basal glabellar lobes 2.4(?), 1.7; maximum width of anterior glabellar lobe, 1.3, 1.1; anterior marginal furrow to rear of glabella on sagittal line, 3.6, —— maximum width between lateral marginal furrows, 3.6, 3.3; rear of glabella to point of maximum width between marginal furrows, projected on sagittal plane, 1.2, 1.6; maximum width of cephalon, 3.8, 3.8; rear of glabella to point of maximum cephalic width, projected on sagittal plane, 2.1, 2.1; rear of glabella to glabellar furrow, in sagittal plane, 1.4, 1.6.

GASTROPODA

Genus HYPSELOCONUS Berkey, 1898

HYPSELOCONUS sp.
Plate 57, figure 45

A single small gastropod, referable to the genus *Hypseloconus* was found during examination of the specimens from Pebble A from SA-EC-17P. It is fairly well preserved, but because of its small size and the lack of additional specimens, it seems best not to attempt to identify it specifically.

The specimen (MCZ 28003) is a curved cone with the apex twisted through about 90 degrees. The apex is bluntly rounded. The aperture is broken but appears to have been round or slightly oval. Outer surface with no visible growth lines or longitudinal striations. Maximum height, 1.8 mm.; estimated apertural diameter before breakage, 2.5 mm.

SPECIES REPORTED BUT NOT CONFIRMED

The following species have been reported from the Rockledge, but an examination of all available collections has failed to confirm their presence. For the sake of completeness, however, they are listed below.

HEMIRHODON SCHUCHERTI Raymond, 1937

Hemirhodon schucherti RAYMOND, 1937, Geol. Soc. America Bull., vol. 48, p. 1104.

The collection from Pebble 2 was asserted by Raymond to contain this species, but a review of the specimens has been made, and no specimens of the genus or species was found.

It is possible that this genus might be present in the Rockledge, for it is of early Dresbachian age, but evidence of its presence is now lacking.

ILLAENURUS BREVICEPS Raymond, 1924

Illaenurus breviceps RAYMOND, 1924, Boston Soc. Nat. History Proc., vol. 37, pp. 445–446, pl. 14, fig. 2.
Illaenurus breviceps RAYMOND, 1937, Geol. Soc. America Bull., vol. 48, pp. 1136, 1138.

This species was originally described from the Trempealeauian Gorge formation. In 1937 Raymond reported it from both the matrix of the Rockledge and from Pebble 2, but no specimens have been recovered during this study that are assignable to it.

STENOPILUS PRONUS Raymond, 1924

Stenopilus pronus RAYMOND, 1924, Boston Soc. Nat. History Proc., vol. 37, p. 420, pl. 13, figs. 6, 7.
Stenopilus pronus RAYMOND, 1937, Geol. Soc. America Bull., vol. 48, p. 1138.

This species was also originally described from the Gorge formation and reported in 1937 from Pebble 2, but again examination of the original material has failed to confirm its presence.

AGNOSTUS INNOCENS Clark, 1924

Agnostus innocens RAYMOND, 1937, Geol. Soc. America Bull., vol. 48, p. 1138.

This species was reported from Pebble 1 at the Rockledge estate, but Raymond's identification of the cephalon of *Acmarhachis* sp. as *Agnostus innocens*, plus the fact the *A. innocens* was found originally in much younger rocks, leads me to doubt that this species is present in the Rockledge.

HUENELLA BILLINGSI (Walcott), 1905

Syntrophia billingsi WALCOTT, 1905, U. S. Nat. Mus. Proc., vol. 28, no. 1395, pp. 291–292.
Huenella billingsi WALCOTT, 1912, U. S. Geol. Survey Mon. 41, vol. 1, pp. 189, 806, vol. 2, pl. 102, figs. 5, 5a–c.

Huenella billingsi SCHUCHERT & COOPER, 1932, Peabody Mus. Nat. History at Yale Univ. Mem., vol. 4, pt. 1, p. 159.

This species was reported in 1925 from the: "Upper Cambrian. In lentile of limestone interbedded in siliceous shales above the Olenellus shales, 1 mile east of Parker's quarry, Georgia Township . . ." This outcrop is now established as part of the Rockledge conglomerate.

No articulate brachiopods were recovered from the Rockledge in the course of this study, so the report of this species must remain unconfirmed.

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JOURNAL OF PALEONTOLOGY, VOL. 26, NO. 3, PP. 484–488, 1 TEXT FIG., MAY, 1952

ADAPTIVE TREND IN EYELINE DEVELOPMENT IN THE OLENELLIDAE

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ABSTRACT—Members of the trilobite family Olenellidae are viewed as probable age equivalents of *Olenellus*. The adaptive trend in eyeline development which is discussed appears to lack any sizeable vertical time component for this reason. Four stages in the progressive development of the ocular plan of *Elliptocephala asaphoides* are defined and taken as a key to homologous development in other members of the Olenellidae. The morphologic changes observed are interpreted as probably corresponding to a series of positional displacements of the optic process, and as being related to adaptive responses of the ocular plan to requirements of habitat and mode of life.

INTRODUCTION

A GENERALIZED statement of the entire process of trilobite optic development (including eyeline development) is given in the views of Beecher and Raymond (Zittel, 1913, p. 706) and an extremely simplified version in Swinnerton (1923; 1946). Reference to the olenellid eyeline is extremely sparse. Warburg (1925, p. 23), discussing olenellid eye ridges, observed that they are very small when present and in some forms are united with posterolateral parts of the frontal lobe, while in others they are separated by a narrow furrow. However, with the exception of *Kjerulfia* and *Holmia*, the same author further noted that for most olenellids "there were hardly any eye ridges." Stubblefield (1936, pp. 421–424) briefly and indirectly, as part of a discussion of cephalic sutures, refers to the olenellid eyeline. The presentations of Beecher, Raymond, and Swinnerton are not directly applicable to the Lower Cambrian Olenellidae and those of Warburg and Stubblefield, while pertinent, do not pursue in any detail the particular problem of olenellid eyeline development as it relates to the family.

The contribution of the present paper is interpretive. It makes free use of previously figured and described olenellid trilobites. A morphologic scale of olenellid eyeline development has not been outlined heretofore and hence applications to diverse members of the family could not be indicated. Such a scale and its applications are given below. On this scale, the zero point corresponds to the most primitive optic development in a figurative sense. Intermediate stages fill the remainder of the hypothetical scale. The author recognizes that the developmental trend elaborated here has wider implications for classification and evolutionary problems related to trilobites and hopes this presentation will stimulate discussion in these areas.

ACKNOWLEDGEMENTS

Study of the trilobite eyeline was begun in 1948 at the suggestion of Professor Frank M. Swartz of the Pennsylvania State College. Professor Norman D. Newell of Columbia University made several helpful suggestions for improving the organization of the first draft. A second draft had the benefit of the constructive criticism of Dr. Christian Poulsen of the Mineralogical Museum, Copenhagen. Rubber casts of Ford's original specimens of *Elliptocephala asaphoides* type numbers 4594–4598; 4605, and casts "H" through "O" were prepared for the writer's use by Mr. A. C. Kilfoyle, Curator of the New York State Museum. In preparation of Figure 1, the facilities of the State University of Iowa, Department of Paleontology, were made available through Professor A. K. Miller, who, together with Mr. Charles Collinson, gave helpful advice on the preparation of the figure. Mr. Len Everett of the State University of Iowa prepared Figure 1 from the author's enlarged tracings of photographs. The writer is pleased to acknowledge this indebtedness.

STRATIGRAPHIC POSITION OF MEMBERS OF THE FAMILY

In the past, the Lower Cambrian has been divided into four zones: the upper *Olenellus* zone, *Callavia* zone, *Elliptocephala* zone, and the lower *Nevadia* zone (Walcott, 1910, p. 250). This requires modification (Poulsen, 1932; Resser and Howell, 1937; Hayes and Howell, 1937; Rasetti, 1948; Tasch, 1949). The *Holmia kjerulfi* zone of Ste. Croix, Poland, and the *Callavia* beds of Comley, England and St. John, New Brunswick, are overlain by *Protolenus* beds and hence are to be viewed as age equivalents. *Callavia* and *Olenellus* occur together in the Robson Peak formation. *Olenellus* and *Paedeumias* have often been found together as in the Parker slate of Vermont and this association probably holds in the *Bonniopsis* horizon in Ellesmere Land (Poulsen, 1946; 1950). *Paedeumias*, *Wanneria*, and *Callavia bicensis* have been found in conglomerate of the same age from Quebec. *Elliptocephala* has been referred to the Olenellus zone (Poulsen, 1932, p. 60).

The occurrence of *Nevadia weeksi* much below *Olenellus* and *Elliptocephala* in the Silver Peak group is well known. Recently, *Nevadia addyensis* was found in the Addy quartzite of Washington. These beds are overlain by the Old Dominion limestone in which a species of *Wanneria* had been previously reported. (Okulitch, 1951, pp. 405–407). Nevertheless, it is difficult to establish *Nevadia*'s basal position among the Olenellidae. Thus, in Raw's (1936, pp. 236–293) Shropshire section, bed Ac_2 yielded both *Callavia callavei* (Lapworth) and *Nevadia cartlandi* (Raw). As discussed above, species of *Callavia* are often associated with those of other olenellids.

Accordingly, in the light of the information which is available at present, *Holmia*, *Callavia*, *Paedeumias*, *Wanneria*, *Elliptocephala* and *Nevadia* are all to be viewed as probable age equivalents of *Olenellus*. The adaptive trend in eyeline development considered below, thus appears to lack any sizeable vertical time component, although species of the above genera might have been separated by geologically short time intervals. The present discussion is restricted to members of the family Olenellidae that are approximate age equivalents of *Olenellus*.

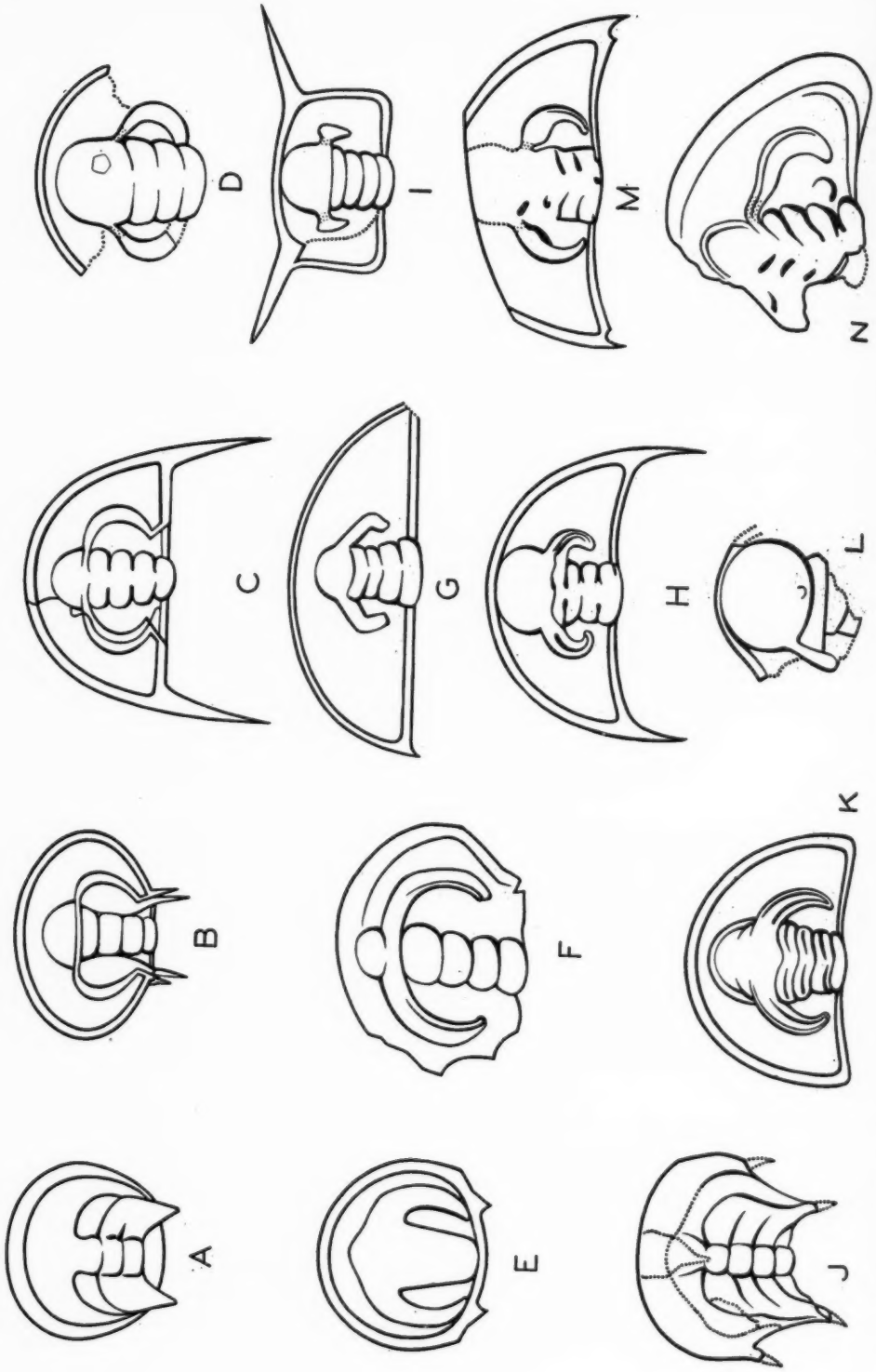
DEFINITION OF THE OLENELLID EYELINE

The term "eyeline" as applied in this paper to the Olenellidae, has not as yet attained precise definition in the literature although it has recently been defined for Cambrian trilobites in general (Howell et al., 1947). Raw's redescription of the family Mesonacidae (Olenellidae) (1936, p. 239) tends to obscure the precise nature of this feature. The palpebral lobes are described as being "more or less continuous with the frontal lobe of the glabella." Størmer (1940–41, p. 99) made specific reference to the Olenellidae in this regard. In the anaprotaspis stage, he states that "the anterior pleura forms the eye lobe which thus differs from the eye ridge occupying only a part of the pleura." However, the same author gave the term "eyeline" an entirely different connotation in his figure of *Holmia kjerulfi* (idem., fig. 14, p. 125) where both an anterior and a posterior eyeline are shown.

For clarity, therefore, "eyeline," "palpebral lobe," "visual integument," "visual surface," are here defined as components of the "ocular plan" of the Olenellidae. When all are present, the components are related as follows: the eyeline leads to the palpebral lobe, the outer surface of which bears the visual integument upon which the visual surface is found (cf. Walcott, 1910, plate 43, fig. 5). In earliest larval stages only, the eyeline represents that portion of the anterior pleura which is here designated "protopalpebral ridge" (see Stage I below). For diverse members of the family, in later larval and adult stages, the eyeline may and frequently does appear as a narrow elevation, thinner, more constricted, pointed or tapered at the place where it issues from the posterior lateral corners of the glabella. The lobe from whence it issues may be either the frontal lobe of the glabella or the first lateral glabellar lobe.

A MORPHOLOGIC SCALE OF EYELINE DEVELOPMENT

Examination of the larval and adult forms of *Elliptocephala asaphoides* discloses several stages of optic development, four of which may serve as a key to similar development in other members of the Olenellidae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(Fig. 1, a–d). Only a few representative examples of olenellid species that clearly illustrate a given stage are cited; there are doubtless many other species, such as the olenellids named by Peach (1892, 1894).

Stage I. Protopalpebral ridge confined to arcuate marginal area of the undifferentiated anterior portion of the cephalon. (An homologous stage is found in *Paedeumias hanseni* and *Holmia kjerulfi*.)

Stage II. Differentiation of part of the cephalon into anterior glabellar lobe and eye lobes united by a median ridge. (A larval *Esmeraldina rowei* shows a similar development. A variation of this stage may be seen in *Nevadia cartlandi* (Walcott, 1910, plate 42, figs. 1, 3) and in *Callavia bicensis*, where two pairs of glabellar furrows appear in front of the median ridge which unites the eye lobes.)

Stage III. Anterior lobe incorporates median ridge connecting eye lobes. (The common olenellid attachment characterizes *Nevadia weeksi*, most species of the genus *Olenellus* and *Wanneria*.)

Stage IV. Slight constriction of the palpebral lobe at or near its point of attachment to the glabella—which is equivalent to the eyeline. (Adults of *Olenellus fremonti* and *Paedeumias robsonensis*, show this feature.) Elongation or extended pinching out of the palpebral lobe towards the glabella—the equivalent of a lengthened eyeline, is illustrated in adults of *Callavia burri*.

ADAPTIVE TREND AND ITS SIGNIFICANCE

Raymond (1920, p. 89) pointed out that if the so-called "nervures" are disqualified, no other evidence has been found of the trilobite nervous system *unless the trilobite eyeline indicates the course of the optic nerve.* It is to be anticipated that if any evidence were found it would be identifiable as some derivative of the basal arthropod type of central nervous system (Borradaile et al., 1949, pp. 310–313, fig. 211). In this connection, the work done on *Limulus* is most suggestive of homologies. Walcott (1910, plate 43, p. 420) indicated the similarities in the visual surface of *Olenellus gilberti* Meek and *Limulus polyphemus*. Recent workers have reaffirmed numerous similarities between the arachnid *Limulus* and the trilobites (exhaustively reviewed by Størmer, 1940, I, pp. 144–268). Gregory (1951, I, p. 62) observes that "the paired eyes in *Limulus* are small but the central nervous system represents a highly "cephalized" derivative of the basal arthropod (*and presumably trilobite*) type" (italics mine). Such confirmation re-enforces an earlier observation that the trilobite eyeline probably indicates the course of the optic nerve, judging from the direction of that nerve in *Limulus* and its relations to the surface features of the cephalothorax (Beecher, 1895, p. 309). Implicit recognition of this interpretation of the trilobite eyeline, may be found in Raw's observation that the eye of *Leptoplastus salteri* (Calloway), migrating backwards and inwards *carried* the eyeline with it (1927, p. 31, my italics).

If we apply this interpretation of the trilobite eyeline to the Olenellidae, then the morphologic changes characteristic of the four stages delineated above, probably correspond to a series of positional displacements of the optic process' "forebrain." These changes may be related to adaptive responses of the ocular plan to the requirements of habitat and mode of life.

EXPLANATION OF FIGURE 1

Schematic enlargements showing four stages of optic development in *Elliptocephala asaphoides* and comparable stages in various members of the Olenellidae.

(*a–d*)—*Elliptocephala asaphoides*, after Ford's drawing (1877, figs. *1–4*; Walcott, 1910, plate 25, figs. *9, 2, 8, 15* respectively) and study of rubber casts of Ford's original specimens; (*a, b*) paraprotaspids; (*c, d*) adult stages.

(*e*)—*Paedeumias hanseni* (Poulsen, 1932, plate 11, fig. *4*), youngest protaspid, and (*j*)—*Holmia kjerulfi*, (Størmer, 1942, II, fig. *4*, p. 61), metaprotaspis or early meraspid stage, are to be compared with (*a*).

(*f*)—*Esmeraldina rowei* (Walcott, 1910, plate 29, fig. *9*), and (*k*)—*Callavia bicensis* (Walcott, 1910, plate 41, fig. *9;* Rasetti, 1948, plate 2, figs. *1–3*) are to be compared with (*b*).

(*g*)—*Nevadia weeksi* (Walcott, 1910, plate 23, fig. *1*), and (*h*)—*Wanneria walcottanus* (Walcott, 1910, plate 30, fig. *2*), and (*l*)-*Olenellus hermani* (Kindle and Tasch, 1948, plate 1, fig. *1*) illustrate the common olenellid attachment seen in (*c*).

(*i*)—*Olenellus fremonti* (Walcott, 1910, plate 37, fig. *9*), (*m*)-*Paedeumias robsonensis* (Burling, 1916, full page figure), and (*n*)-*Callavia burri* (Walcott, 1910, plate 28, fig. *10*) are to be compared with (*d*).

In series (*d, i, m, n*) stippling indicates formation of a clearly distinguished eyeline.

ADDENDUM

Since this paper was written and while it was awaiting publication, certain additional information was forthcoming. Lamont (Geol. Mag., 1951, vol. 88, pp. 295–296) notes that in *Olenellus* cf. *gilberti* Meek and in *Callavia bicensis* Walcott (cf. fig. 1 (k)) the arcuate eyes join on to "what is here regarded as the third segment of the pseudofrontal lobe." *Callavia bicensis* Walcott illustrates a variation of Stage II of the morphologic scale. Lamont's "third segment" is here interpreted to be "a median ridge which unites the eye lobes" and to be homologous to equivalent development in *Elliptocephala asaphoides* (fig. 1 (b)).

Patten and Redenbaugh (Jour. Morph., 1900, vol. 16, Part 2, pp. 91–200) present a view of the entire nervous system of *Limulus polyphemus* from the neural side and show both lateral nerve and lateral eye (plate 6, and cf., plates 7 and 8). The entire course of the lateral eye nerve is succinctly given below (idem: p. 139):

> Lateral eye nerves arise from the large optic ganglia upon the haemal side of the cerebral lobes, pass forward median to the tergo-coxal muscles of the chelicerae, turn outward around the anterior outer corners of the entocoxites of the second pair of appendages and then pass backward to the lateral eye. The distal extremity breaks up into two small branches and a large one. The large one passes directly to the retina of the lateral eye; the two smaller ones pass farther backward to a pigmented body beneath the retina. A large blood vessel encloses the lateral eye nerve for the greater part of its course and is continued beyond the lateral eye. . . . .

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JOURNAL OF PALEONTOLOGY, VOL. 26, NO. 3, PP. 489–500, PL. 58, 4 TEXT FIGS., MAY 1952

JAWS AND TEETH OF AMERICAN XENACANTH SHARKS

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ABSTRACT—Study of American xenacanth sharks has been largely restricted to description of new material, with resultant multiplication of genera and species. Comparison of earlier described teeth and jaws with more recently discovered material from younger Permian beds indicates that American xenacanths from Pennsylvanian and Permian strata can probably be assigned to a single genus, *Xenacanthus*, and to three species, *compressus*, from the Pennsylvanian of the midwest, and *texensis* and *platypternus*, from the Permian of Texas. Of the two Permian species, *texensis* is typical of the Wichita, and *platypternus* is common in the Clear Fork, but apparently the two never occur together.

A number of apparently primitive morphological features of xenacanth jaws and suspensory apparatus are discussed.

INTRODUCTION

SHARKS of the genus *Xenacanthus*[1] are common in the bone-bearing, Permocarboniferous redbeds of north-central Texas, and occur in deposits of similar age in other parts of the United States. Many specimens have come from the middle west and the northern Appalachian region. Teeth and spines are most commonly encountered, but occasional finds of calcified cranial and visceral elements have been made. Xenacanth remains are well-known also from Carboniferous and Permian deposits of Europe.

Although the European specimens have been extensively studied during the past one hundred years, much less attention has been paid to American material. Cope (1884), in a discussion of his genus *Didymodus*, gave a fairly comprehensive account of the skull of *X. texensis*, and the original description of *X. platypternus* appeared as a sort of appendix to this article. In 1904, Broili gave a description of chondrocranium and jaws of *X. platypternus*, which he called *Diacranodus texensis* as a result of misinterpreting Cope's 1884 article. Broili's account of the jaws was not complete because of poor preservation of that part of his material.

The present paper is based essentially upon eight more or less complete sets of well-preserved jaw and hyoid arches of American xenacanths, five of which have teeth associated with them. Its aim is to supplement Broili's descriptive work with regard to the jaws of *X. platypternus*, and to try to straighten out the taxonomic confusion that ensued from his misinterpretation of Cope's paper of 1884. In addition, jaws and teeth of *X. texensis* and *X. platypternus* are considered both morphologically and with respect to their occurrence. Finally, some observations are made regarding the nature of amphistyly as it is expressed in the xenacanths.

The writer wishes to express his gratitude to Dr. E. C. Olson of The University of Chicago for his critical guidance of this study. Thanks are also due to Dr. Robert Denison and Mr. Bryan Patterson of the Chicago Natural History Museum for their interest and advice, and to Dr. J. A. Wilson of the University of Texas, for the opportunity of studying the xenacanth material in his custody. Drawings are by Mr. John Conrad Hanson, Staff Artist, Chicago Natural History Museum.

MATERIAL

The specimens upon which this study is based are listed in Table 1. All except UT 40019 and UT 4003028 are in the collections of the Chicago Natural History Museum. Specimens UT 40019 and UT 4003028 are in the paleontological collections of the University of Texas, at Austin.

[1] Following Olson (1946), the present writer refers all American material which has been assigned to genera based on teeth or spines, to *Xenacanthus* Beyrich. Among these, the following genera are discussed in this paper: *Orthacanthus* Agassiz, *Diplodus* Agassiz, *Pleuracanthus* Agassiz, *Dittodus* Owen, and *Didymodus* Cope.

TABLE 1—SPECIMENS STUDIED

Specimen No.	Locality	Formation	Matrix	Element
CNHM UF 113	E side of Middle Coffee Creek, on old Seymour-Vernon hwy, about 1½ mi., N of Lake Kemp, Baylor Co., Texas	Arroyo	Hard, red, calcareous crust.	R and L Mc, R and L Pq, R and L Ch, L Hm, and indet. branchial frags. 5 teeth.
CNHM UF 83	"Near Seymour," Baylor Co., Tex.	Probably Arroyo	Hematitic, botryoidal red crust.	R Mc, R Pq, R Ch, L Hm, and 1 teeth.
CNHM UF 86	Tit Mt., Dundee, Archer Co., Tex.	Belle Plains	Yellow-gray fine-grained sandstone.	Both Mc, both Pq, both Ch, L Hm, chondrocranium, and misc. branchial elements.
UT 40019	3½ mi. W of Rattlesnake Canyon, Archer Co., Tex.	same	Hard, red crust.	Both Mc, both Pq, both Ch, chondrocranium. 65 teeth.
UT 4003028	Rattlesnake Canyon, Archer Co., Tex.	same	same	Fragment of Mc, with teeth in situ.
CNHM UF 1048	N Fork, Little Wichita R., S of Fulda, E Baylor Co., Tex.	same	Gray to red-brown sandstone.	L Ch
CNHM UF 1049	same	same	same	R Mc, occipital region of chondrocranium.
CNHM UF 1904	SW ¼, NW ¼, sec 30, T4N, R4E, Marion Co., Ill.	Plant-bearing beds of Pennsylvanian age. No fm. name. See Olson, 1946.	Gray shale	Fragments of very large, well-calcified chondrocranium and jaws. More than 20 teeth.[2]

Stratigraphic position of exposures at the listed localities is based upon data given by Romer (1935) and Romer and Price (1940).

The term "crust," as used in Table 1, refers to a hard, nodular coating found on many specimens from the Texas Permian, which contains a higher proportion of calcareous or hematitic cement than does the surrounding rock.

Abbreviations used in Table 1 are: Ch, ceratohyal cartilage; Hm, hyomandibular cartilage; Mc, Meckel's cartilage; and Pq, palatoquadrate cartilage.

MORPHOLOGY

Palatoquadrate cartilage.—The xenacanth palatoquadrate (Plate 58, fig. 1, A, C), in general outline, consists of a posterior quadrate or otic portion and an anterior palatine or orbital portion, which resemble those of the upper jaws of the living Notidanidae.

The quadrate occupies more than half of the element, and is elevated behind the orbit to almost twice the height of the palatine portion. The anterior border of the quadrate forms the posterior edge of the orbit, and at its highest point is expanded into an otic process, which articulates with the postorbital process of the chondrocranium. Posterior to the otic process, the dorsoposterior margin of the element curves gently downward and backward, describing a quarter circle; the margin is crimped into a tight flexure, which is convex laterally and forms a reinforcing rim on the quadrate portion. At the posterior extremity, the marginal rim is consolidated into a stem-like articular process (cf. Broili, 1904), and is expanded slightly to become a condyle for articulation with the lower jaw. Immediately in front of the articular process, on the ventral margin of the medial face of the palatoquadrate, is a broad, shallow socket whose function is discussed below.

The surface of the quadrate portion has the appearance of having been folded along a line curving from behind the orbit down to the articular process. The lower half of the surface appears to have been displaced inward with respect to the upper half, forming a fossa for reception of the adductor mandibularis muscle, which doubtless had its origin on the dorsal edge of the fossa.

The ventral margin of the palatoquadrate is unexpanded and forms a sigmoid curve, concave downward in the quadrate region

[2] The beds in which UF 1904 was found are almost entirely barren of vertebrate remains (Olson, 1946); the isolated condition of the specimen is cited as evidence that it represents a single individual.

and convex downward in the palatine region. The ventral two-thirds of the palatine portion is strongly arched through its whole length, along an anteroposterior axis. This arching forms an internal longitudinal furrow, which occupies the entire length of the palatine portion and extends a short distance into the anteroventral corner of the quadrate; it is the dental furrow, which housed replacing teeth during the life of the animal.

The thin-edged dorsal margin of the palatine portion, rising above the dental furrow, forms the ventral margin of the orbit; curving upward anterior to the orbit the margin forms a bladelike eminence, the orbital process. The orbital process evidently made contact with the chondrocranium in the anterior half of the orbit. There is no evidence of a true articulation in this region of the braincase, and apparently the orbital process merely lay against the wall of the orbit, held in place by encapsulating ligaments, much as in modern true sharks. There are three vertical ridges on the internal face of the orbital process, which may possibly have served to help reduce slippage at this simple contact between upper jaws and braincase.

In general, the upper jaws of xenacanths bear a close resemblance to those of *Cladodus wildungensis* (cf. Gross, 1937, 1938), markedly so with respect to outline and cross section. The chief difference lies in the nature of the dental furrow, which is simple in the xenacanths but is subdivided into shallow vertical grooves in *C. wildungensis*. In UT 40019, however, broad, shallow vertical grooves are apparent in the dental furrow of Meckel's cartilage but not in the palatoquadrate. These grooves differ from the *Cladodus* type in that there are only three of them in the whole length of the dental furrow; size of teeth associated with UT 40019 indicates that each vertical groove must have held several vertical rows of teeth. In Gross' specimens of *C. wildungensis* there are from five to eight vertical grooves in each dental furrow, and each held only one vertical row of teeth. Another difference is that *C. wildungensis* apparently has no otic process, although the otic expansion of the quadrate portion is well-developed. The lack of an otic process is not certain, however; Jaekel describes one in the type specimen but Gross states that it is lacking in this and in one other specimen at his disposal.

Meckel's cartilage.—The depth of Meckel's cartilage (Plate 58, fig. 2, A, C) is essentially constant from the posterior end to the midpoint; anteriorly the ventral margin slants gently upward, so that the symphysial region is less than half as deep as the articular region. The internal face of the tapering portion bears the prominent dental furrow. The thin margin which bore functional teeth rises a short distance above the dorsal surface of the dental furrow and corresponds in length and position with its counterpart on the palatoquadrate.

The lower jaw is much more massive than the upper. The lateral face of its posterior two-thirds is excavated to form a fossa adductor mandibularis, leaving the ventrolateral margin standing out as a ridge upon which the adductor mandibularis muscle inserted during life. The ventromesial margin is also somewhat expanded, and is separated slightly from the ventrolateral margin by a shallow groove. The two ventral marginal expansions merge in the massive anterior third of the jaw, which is almost round in cross-section. Posteriorly the two expansions also fuse to form a single, slightly expanded rim in the articular region. The double ventral expansion resembles somewhat the condition described in *Chlamydoselachus* by Allis (1923), but the posterior margin angles sharply upward, and is more like that of the pentanchid sharks than it is like *Chlamydoselachus*.

The articular region is situated on the dorsal margin of the element, a little anterior to the posterior end. The chief articular facet is a posterolateral concavity, the articular cotylus, which is supported by an expansion on the outer face of Meckel's cartilage, and which receives the articular process of the palatoquadrate. Anterior to the articular cotylus, the coronoid margin is produced into a strong, medially- and posteriorly-directed mandibular knob, which in *Xenacanthus* appears to fit into the shallow concavity on the inner face of the palatoquadrate, in front of the articular process.

Viewed from above, Meckel's cartilage curves evenly from the articular region to

the symphysis, the left and right rami together forming a broad, shallow U, a common pattern in sharks of predaceous habit. The tooth-bearing margins flare outward somewhat from the curve of the lower part of the jaws, giving a bowl-shaped appearance to the anterior end. Distortion caused by lateral compression has occurred in nearly half of the specimens studied, which obscures the bowl-like flare, and indeed may obliterate the characteristic U-shape.

Hyoid arch.—The elements of the hyoid arch, like those of the mandibular arch, are well preserved in the specimens at hand, but unfortunately were disarticulated and scattered at the death of the individuals. Other described specimens (e.g., see Cope, 1884, and Broili, 1904) have been preserved in slabs, with the second visceral arch partially or completely hidden by the first, so that relationships between the two are obscure. In the following description, which is to be regarded as tentative with respect to both identification and orientation of the limbs of the hyoid arch, the hyomandibular is designated as such for two reasons: one, that it is the smaller of two elements in the second arch, as is generally the case in elasmobranchs; and two, its distal lateral surface resembles most closely the corresponding surface of the hyomandibular figured by Broili (1904). Broili's specimen is well preserved and retains a considerable degree of articulation.

The hyomandibular (Plate 58, fig. 1, B) is a thin, flat blade, without prominent marginal expansions or ridges. Broadest in its forwardly-curved proximal third, it tapers gradually downward to the distal end, which is slightly heavier than the rest of the element and bears a groove oriented parallel with the plane of the flat proximal end, evidently for articulation with the ceratohyal. Lateral to this groove the anterior margin is produced into a conical process. There is no articular surface, as such, developed at the proximal end, but it is probable that the forward-curving posterior margin lay against the otic region of the chondrocranium and was secured there by ligaments, as in the notidanids. In the otic region the cranial roof extends laterally beyond the wall of the braincase, forming a shallow longitudinal groove which is located so as to receive the proximal end of the hyomandibular. The hyomandibular probably did not function as a suspensor in the xenacanths; in its length and slenderness it resembles the hyomandibular of the recent Notidanoidea, which is non-suspensorial.

At the anteroproximal extremity there is a process of rather variable development. It is either attached to or part of the proximal end of the cartilage, and is most clearly visible in lateral aspect, where it appears as a flat plate. Although it varies in size in the three hyomandibulars at hand, it is a distinct entity in all of them.

On the distal surfaces are variously developed ridges and humps of poorly calcified material. They appear merely to adhere to the hyomandibular and not to be integral parts of this element, and it is believed that some of them, at least, are remnants of the cartilaginous rays that arose from the hyomandibular to support gill flaps.

The ceratohyal cartilage (plate 58, fig. 2, B) has much the same general outline as the hyomandibular, being curved upward in its proximal third, where it is widest, and tapering gradually in a distal direction. It is about one-third again as large as the hyomandibular, and is characterized by three processes on its external face. One process forms the external edge of the articular groove at the proximal end; it is laterally compressed and slender, and is directed dorsally. The second process is a large, rounded boss, located anteroventrally to the first, near the posteroventral curve of the cartilage. The third is a ridge that occupies the distal third of the dorsal half of the external face, rising gradually out of the external face and ending distally in a slight convexity.

Jaw articulation and suspension (fig. 1, A, B, C).—Configuration of the articular region of Meckel's cartilage is a remarkably constant feature in the sharks. The posterolateral articular cotylus for reception of the articular process of the palatoquadrate, together with the prominent anteromedial mandibular knob, is found in *Chlamydoselachus*, the Notidanidae, *Heterodontus*, and in most if not all of the pentanchid sharks, as well as in *Xenacanthus*. Among other extinct forms, *Cladodus wildungensis* and the

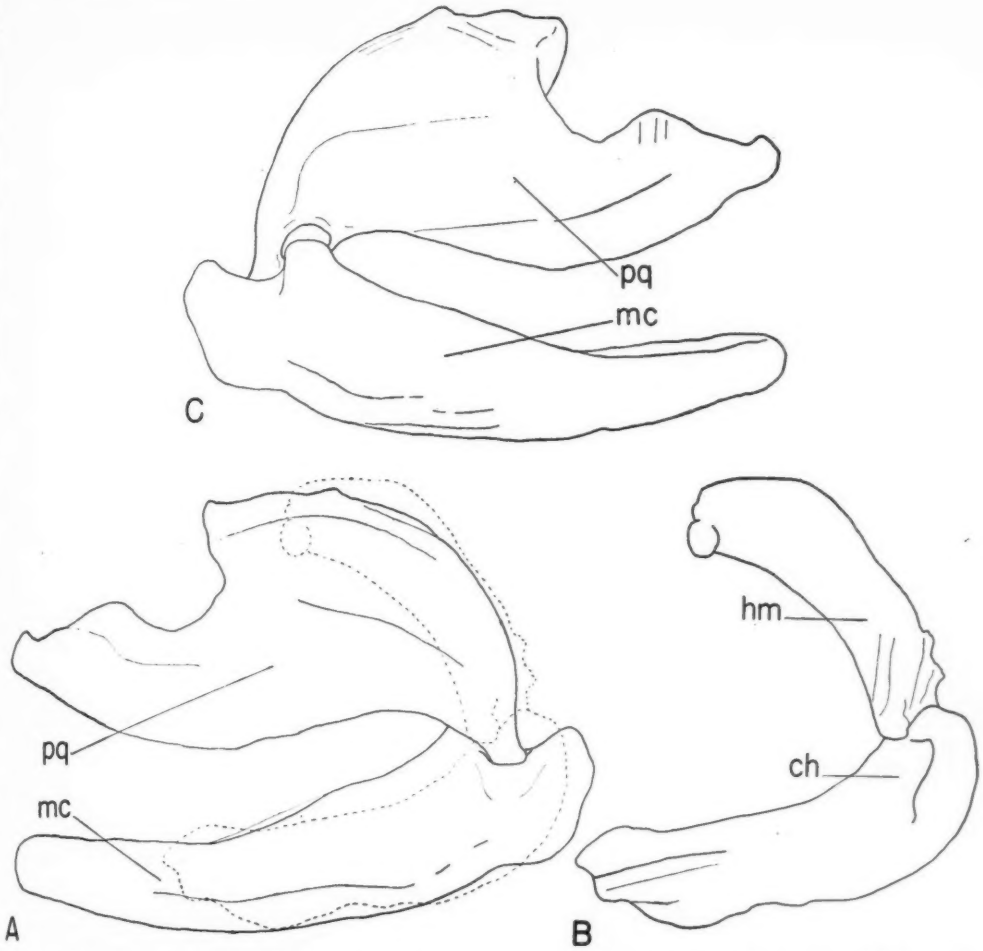

FIG. 1—Restoration of jaw and hyoid arch relationships in *Xenacanthus* (×$\frac{1}{4}$). Based chiefly upon CNHM UF 113 (*X. platypternus*); additional details from CNHM UF 86 (*X. texensis*). ch, ceratohyal cartilage; hm, hyomandibular cartilage; mc, Meckel's cartilage; pq, palatoquadrate cartilage. (A) External aspect of mandibular arch; position of hyoid arch shown by broken lines. (B) External aspect of hyoid arch. (C) Internal aspect of mandibular arch, showing articulation between upper and lower jaws.

hybodont, *Protacrodus vetustus*, exhibit a similar condition, according to descriptions and figures by Gross (1937, 1938). Apparently the same arrangement obtains in more primitive groups than the elasmobranchs, for Jaekel (1928) and Watson (1937), in figures of the jaws of *Acanthodes bronni*, show a well-developed process on the lower jaw in front of the articular cotylus. It is evidently not such a constant feature in the acanthodians as in the elasmobranchs, however.

The mandibular knob is in general called an auxiliary articular facet. Gegenbaur (1872) considered the cotylus to have been the site of primitive articulation between the undifferentiated members of the first visceral arch, and the mandibular knob to have evolved during the development of the biting function of the jaws. In any case, the primitive condition of selachian jaw articulation appears to have involved a double joint.

Chlamydoselachus, the notidanids, and *Heterodontus* possess a definite concavity on the palatoquadrate for reception of the

mandibular knob. In these forms the two facets of the auxiliary articulation are separated by a spongy pad of connective tissue, in contrast to the direct contact of smooth cartilage surfaces in the posterolateral or primary joint. The two articulations are nearly side by side in position; in *Chlamydoselachus* this arrangement is brought about by backward prolongation of the mandibular knob, and in the others it is accomplished by outward rotation of the posterior ends of the jaws, which carries the primary joint slightly forward so that it lies immediately external to the mandibular knob. The xenacanths have a well-developed quadrate concavity, and Gross (1938) states that in *C. wildungensis* there is possibly a groove on the palatoquadrate for reception of the mandibular knob. Unfortunately, the articular surfaces of *C. wildungensis* described by him are poorly preserved. At any rate, in the xenacanths and *Cladodus* the mandibular knob is located more anteriorly than medially with respect to the primary articulation. In this position it would appear to interfere with free movement of the jaws if its function were that of an auxiliary joint. However, if the facets were attached to each other by spongy connective tissue, as in living forms, there would be enough play between them to prevent any interference with jaw action. The antero-posterior orientation of mandibular knob and articular cotylus appears to be primitive, in contrast to the side-by-side orientation of modern forms.

In most of the pentanchid sharks, the quadrate concavity is poorly developed; in *Galeus* and *Mustelus* among the galeoids (Gegenbauer, 1872), and in *Squalus* among the squaloids, for example, it is lacking, and the mandibular knob glides over a small facet on the palatoquadrate. It is interesting to note that in living forms with well-developed quadrate concavities there is no direct ligamentous connection between the mandibular knob and the hyomandibular cartilage, although in *Heterodontus* a process of the latter abuts against the mandibular knob. In more advanced forms, in which the quadrate concavity is poorly developed or lacking, a strong ligament connects the mandibular knob with the hyomandibular cartilage. In general, sharks with a concavity on the palatoquadrate, for articulation with the mandibular knob, have a slender, non-suspensory hyomandibular, and those without a quadrate concavity have a short, stout, suspensory hyomandibular. The function of the mandibular knob appears to be directly related to the degree of functional amphistyly in the sharks; it acts as an auxiliary jaw articulation in forms with non-suspensory hyomandibular and accompanying close articulation between the posterior end of the palatoquadrate and the braincase, and as an anchor point for support by the suspensory hyomandibular in forms with no posterior braincase-palatoquadrate articulation.

The peculiarly crescentic outline of the otic part of the palatoquadrate, typical of the xenacanths, is common to several other groups of amphistylic sharks, which are not necessarily closely related. It occurs in cases where amphistyly is effected by means of an otic process, and is closely associated with a non-suspensorial hyomandibular. The striking resemblance between palatoquadrates of *Xenacanthus* and the notidanids is probably only superficial; important differences exist between the two groups with respect to palatoquadrate braincase relationships. In the first place, the orbital process of the xenacanth palatoquadrate articulates with the anterior wall of the orbit, as does that of *Cladodus*, in contrast to the more posterior position of the articulation in all of the Recent forms. Associated with this difference is the greater length of the palatine region, or that part of the palatoquadrate anterior to the orbital process, in Recent forms, as compared with the corresponding region in known Paleozoic sharks. In the second place, the palatoquadrate of *Xenacanthus* is shorter than Meckel's cartilage, and there appears to have been no symphysial connection between the two upper jaws.

Perhaps the best explanation to date of the origin of the shark type of hyostylic jaw suspension is that it was derived from a (hypothetical) primitive "orbitostylic" condition (Holmgren, 1941, 1943). In this phase the palatoquadrate was connected, through ligaments or muscles, with the hyomandibular, which, however, was not yet morphologically a suspensor (i.e., it was still long

and slender, had no especial suspensory processes, and had no more than ligamentous connection with the chondrocranium). According to this theory, no ancestor of the modern hyostylic sharks need have had amphistylic jaw suspension that involved an otic process; the type of amphistyly shown by the Notidanidae probably developed secondarily, from a stage represented by the condition found in *Chlamydoselachus*.

Whether this is true or whether the Notidanidae have inherited their type of jaw suspension directly from Paleozoic ancestors cannot be determined with certainty, but Holmgren believes that amphistyly as developed in the xenacanths is probably primitive. The nature of the xenacanth hyomandibular is here interpreted as confirmation of this conclusion. In Recent sharks the hyomandibular is composed of a single cartilage which chondrifies from two initial sites, a major one, which is interpreted by Holmgren as representing the ancestral epihyal element, and a minor one, located proximally to the major site, which corresponds to the former pharyngeohyal. The proximal process of the xenacanth hyomandibular, described above, is believed by the present writer to be a remnant of the pharyngeohyal element that has become fused to the epihyal, or hyomandibular proper, but which has not completely lost its identity. If this interpretation is correct, the condition of the xenacanth hyomandibular is the most primitive known, for in no other adult shark, living or fossil, is any trace of the pharyngeohyal recognizable. Amphistyly that is associated with a well-developed otic process accompanies an extremely unspecialized hyomandibular in the xenacanths; therefore it is probably primitive in that group, rather than secondarily developed.

TEETH AND TAXONOMY

The xenacanth tooth (fig. 2) consists of a circular or elliptical base which bears two large cusps on the labial margin[3] of its apical surface. The cusps are laterally compressed in many specimens; these have carinated edges. The bases of the cusps are in a line parallel with the tooth-bearing margin of the jaw. There is, as a rule, a small cuspule between the two larger cusps, although there may be none, or more than one. Most teeth have a flat, clearly-defined button on the apical surface of the base, in a lingual position with respect to the cuspule. The basal surface bears a more or less well-developed tubercle on its labial margin.

Fritsch (1890) describes the teeth of *X. decheni* as being arranged in five horizontal rows on each jaw element, and numbering about 300 in all. Tooth arrangement and the pattern of the dental furrow suggest a similarity between the habit of the teeth in *Xenacanthus* and that found in more modern sharks. It is reasonable to assume that teeth of the outer horizontal row were functional, while those of the four inner rows

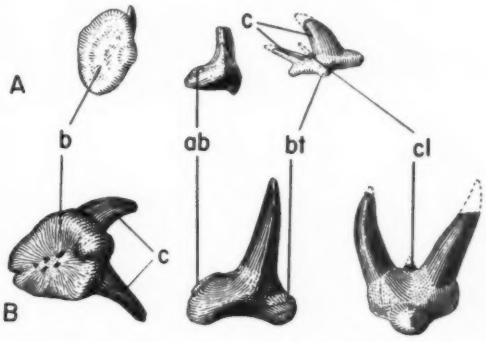

FIG. 2—Xenacanth teeth (×1). ab, apical button; b, base; bt, basal tubercle; c, cusps; cl, cuspule. (A) CNHM UF 113, *X. platypternus;* basal, posterior, and labial aspects. (B) CNHM UF 1904, *X. compressus;* basal, anterior, and labial aspects.

[3] Conventionally referred to in the literature as the anterior margin; correspondingly, the region designated as lingual in this paper is called posterior in the literature. Further, directions described as anterior and posterior here are called lateral in the bulk of the literature. The convention of calling the cusp-bearing margin of the xenacanth tooth anterior, etc., probably arose when its correct orientation with respect to the jaw was unknown. Since it has long been well-documented that the teeth were oriented in life with their cusps aligned parallel with the jaw margin that bore them, and with the cusped margin labial, the present writer believes that it is high time for the terminology to be changed accordingly. For evidence in support of this suggested change, see fig. 6, this paper, and Fritsch (1890, Pl. 102, fig. 1).

were replacement teeth (cf. fig. 3). Fritsch illustrates a sort of tubercle-and-button articulation between the teeth (1890, fig. 232). He explains the figure as a "somewhat schematic" side view of adjoining teeth in one horizontal row, showing each tooth with its "anterior" tubercle resting on the "posterior" button of its neighbor. Using the orientation suggested in the present paper, the situation becomes more comprehensible. With the basal tubercle being labial and the apical button lingual, the illustration becomes one of a vertical row of replacement teeth, with each tooth of any vertical row articulated with those adjacent

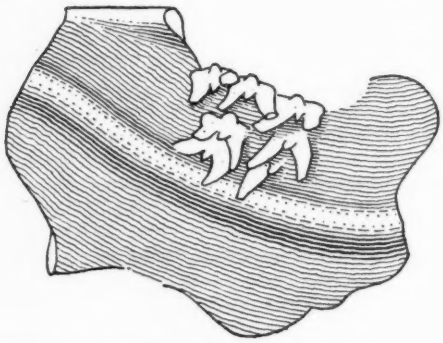

FIG. 3—UT 4003028 (*X. texensis*). ×¾. Internal aspects of portion of left Meckel's cartilage, at posterior end of dental furrow, showing a part of three rows of replacement teeth. First row of replacement teeth, and functional marginal teeth lacking.

to it by means of tubercle and button. In recent sharks, the fibrous connective tissue that supports the teeth is known to move slowly up the side of the dental furrow, so that replacement teeth are carried with it bodily, to become erect and functional when they reach the jaw margin. Articulation between teeth in the xenacanths may be simply a means of augmenting a similar function of the fibrous gum tissue in that group.

Of the jaw cartilages upon which this study is based, four of the specimens have teeth associated with them. The teeth with UT 40019 and UT 4003028 can be assigned to *X. texensis* (Cope); the literature concerning this species is confused, and needs clarification. Cope (1884) described a suite of twelve skulls from the Texas Permian, and referred them to *Didymodus compressus* (Newb.) on the basis of teeth associated with them. In the type description of "*Diplodus*" *compressus*, Newberry (1856) states that the teeth are

> of moderate size, base small. Lateral denticles [cusps] unequally spreading, compressed, with acute points and strongly crenulated edges. Central denticle [cuspule] very small, acute, compressed, finely crenulated on margins.

Described in the same paper are two other species, *D. latus* and *D. gracilis*. The former differs from *D. compressus* chiefly in being larger, and the latter in being smaller, although gradational sizes occur (Newberry, 1866, 1873). *D. gracilis* ranges from 5 to 15 mm. in height, *D. compressus* from 7.5 to 15 mm., and *D. latus* up to 22.5 mm. (exceptionally 25 to 40 mm.). Other differences pointed out by Newberry include increasingly larger proportionate size of base, increasing lateral compression and decreasing slenderness of cusps, and increasing degree of crenulation of cusps, in larger specimens. Also, in the larger specimens the denticle appears less prominent. All three possess a prominent basal tubercle which, while not described, is figured by Newberry in a later work (1875). All three species occur in the cannel coal at Linton, Ohio, and in the "Upper Coal Measures," Posey County, Indiana. Newberry admits the possibility that the three forms may be conspecific, and Woodward (1889) suggests that smaller teeth are actually from smaller individuals of one species.

Another possibility is that several different sizes of teeth may have come from one individual, as in modern sharks, and the present writer has at hand a series of teeth from a single individual (UF 1904) that illustrates exactly this condition. The teeth correspond in all respects, except possibly in degree of crenulation of cusps and cuspule, to the *gracilis-compressus-latus* size series; they range from a minimum height of less than 10 mm. to a maximum of more than 20 mm. This is strong indication that *D. gracilis*, *D. compressus*, and *D. latus* are conspecific; *gracilis* and *latus* are here regarded as synonyms of *compressus*.

Cope did not describe the teeth of the specimens from Texas, but figured one (1884, Pl. I, fig. 5) and labeled it "*Did. com-*

pressus (Newb.)," which it clearly resembles. Later (1890) he referred this series to a new species, but without further description. Since then the name *D. texensis* has become fixed in the literature, although not always correctly applied, as will be shown below.

Xenacanthus texensis, of the Wichita group of the Texas Permian, bears a strong morphological resemblance to *X. compressus* of the Pennsylvanian of Illinois, Indiana, and Ohio. Its size range is similar; in both forms the base is wider than long and triangular in outline, with thick, rounded edges and a prominent basal tubercle and apical button. The cusps are generally similar in both forms, but in *X. texensis* they are more distinctly and coarsely crenulate and more laterally compressed in teeth of corresponding size. An interesting difference appears in the condition of the cuspule. In *X. compressus* it is consistently small, and lacking in occasional specimens; in *X. texensis* a similar situation obtains, but in addition, about one tooth out of four or five will carry two or three cuspules instead of the usual one.

It is admitted that the above morphological criteria are hardly adequate of themselves to differentiate two species. However, the midwestern deposits in which *X. compressus* occurs are known to be considerably older than the Texas beds in which *X. texensis* occurs, and this, perhaps augmented by the fact of geographical separation, indicates that the two species are distinct, although closely related.

The teeth associated with UF 113 and UF 83 differ clearly from those described above as *X. texensis*, and correspond closely to *X. platypternus* (Cope); Cope's description (1884) of the teeth of this species reads in part:

> ... the posterior [lingual] portion [of the base] is a flat, thin-edge plate, wider than long. It carries a button but no notch. There is a minute median denticle [cuspule].

His material consisted of several teeth associated with a partial Meckel's cartilage, which had no mandibular knob. Broili (1904), erroneously calling the species *Diacranodus*[4] *texensis*, supplemented Cope's description to include the chondrocranium and more nearly complete jaw elements; he described a mandibular knob on Meckel's cartilage, pointing out that the prominence was probably missing from the type specimen on account of poor preservation. With respect to the teeth, he showed that both cusps were curved backward to about the same extent, rather than being apically divergent as Cope had restored them. However, it is certain that both writers were discussing the same species, Broili's clear description and numerous figures leaving no doubt on this score.

FIG. 4—CNHM UF (*X. texensis*). ×¾. Xenacanth teeth in labial aspect, showing variability of cuspule.

The type description of *X. platypternus* is appended to a long, detailed description and discussion of the genus *Didymodus* (Cope, 1884). The main part of the paper is devoted to the suite of 12 skulls and associated teeth, which were at that time referred by Cope to *D. compressus*, as mentioned above.

Broili (1904), however, apparently thought that the teeth associated with the suite of 12 skulls were of the form described above as *X. platypternus* (i.e., with thin, plate-like base and cusps curved in a similar direction). On this basis he thought that Cope had made a mistake in calling them "*D.*" *compressus*, hence his designation of "*D. compressus* Cope non Newb." Then, Broili interpreted the type description of "*D.*" *platypternus* as pertaining to a form of tooth very similar to that associated with the suite of 12 skulls, and distinguished from it only by the presence of a basal lingual notch. He claimed that this was insufficient grounds for separation of the two species and made "*D.*" *platypternus* synonymous with "*D.*" *texensis* (Cope). But this is not the case; the teeth associated with the 12 skulls have thick, round-edged bases and apically divergent cusps, and are not at all

[4] Garman, 1885.

like the type of *platypternus*. Cope's separation of the two species, *texensis* and *platypternus* is based on the entirely different forms of teeth in the two groups.

Thus, correcting Broili's misapprehension of Cope's original description while accepting his excellent supplementary material, we find that the specimens assigned by Cope to "*D.*" *compressus* (Newb.) and later to "*D.*" *texensis* Cope are truly *X. texensis* (Cope), and that *X. platypternus* is a valid species. The specimens assigned to "*D.*" *texensis* by Broili are actually *X. platypternus*.

Teeth of *X. texensis* and *X. platypternus* differ strikingly in shape of base; in the former the base is thick, massive, wider than long, and bears a strong basal tubercle, while in the latter it is thin-edged and plate-like, longer than wide, and bears a very small, though usually clearly defined basal tubercle. The cusps of *X. texensis* are apically divergent, with crenulated edges, and are more compressed laterally than are those of *X. platypternus*, while the cusps of the latter are curved equally backward and are non-crenulated. Difference in cuspule development between the two species is pronounced. In *X. texensis* the cuspule, when present, is always small; in about one out of four or five specimens it is double or triple, and in about one out of ten it is lacking entirely. In *X. platypternus*, on the other hand, the cuspule is always present and always single; although slender it is long and sharp.

The two species apparently never occur together; *X. texensis* is confined to the Wichita group of the Texas Permian, and *X. platypternus* to the Clear Fork. Except for UF 83, which is labeled merely "near Seymour" and may be from the Clyde, *X. platypternus* has been reported only from the Arroyo formation of the Clear Fork group. *X. texensis* is evidently descended from and closely related to *X. compressus* (Newb.) of the midwest Pennsylvanian, as shown by a comparison of teeth in the two species. On the basis of the numerous differences between teeth of *X. texensis* and *X. platypternus* (and the different evolutionary trends indicated by the cuspules of the two Texas species), it is concluded that *platypternus* is not descended from *texensis*, but from an unknown contemporary of the latter. Terrestrial sediments of the Clear Fork in general appear to have been laid down in more rapidly running water than do those of the Wichita, and since *X. platypternus* is more commonly found associated with channel conglomerates than is *X. texensis*, it is suggested that the former is a stream-dwelling immigrant that has replaced the pond-dwelling *X. texensis* in the Texas collecting area in Clear Fork time.

The differences in dentition between *X. texensis* and *X. platypternus* are paralleled closely in the European genera *Orthacanthus* on one hand, and *Xenacanthus* (including its synonym *Pleuracanthus*) on the other (Fritsch, 1889). Teeth of *Orthacanthus* are in general larger, with more massive base, smaller cuspule, and crenulated cusps, in contrast to the plate-like base, prominent cuspule, and non-crenulated cusps of *Xenacanthus*. In the European forms, however, generic distinction between *Orthacanthus* and *Xenacanthus* is also supported by evidence from spines and cartilaginous skeletal material, in addition to teeth, which is, so far as known, not the case in the American species.

Although *X. texensis* and *X. platypternus* differ widely in the form of their teeth, the proportions of the jaw elements in the two species are remarkably similar. Articular faces and processes are also developed to approximately the same degree; about the only observable difference is the development in *X. texensis* of three vertical hollows on the dorsal wall of the dental furrow of Meckel's cartilage, and the complete lack of this feature in *X. platypternus*. The high degree of similarity between jaw and hyoid elements in the two species tends to rule out the possibility that the observed differences in the teeth might be of generic value. It is true that two genera of the Xenacanthidae that lived under similar environmental conditions might be convergent in jaw structure, but to use this explanation to account for similarity in the forms under consideration would be to base generic distinction upon teeth alone, a highly unsafe procedure, considering the great variability in teeth between many groups of sharks that are known to be closely related. Any consideration of generic differences between the two

types discussed here should await comparison of at least chondrocrania and spines in addition to parts here discussed; ideally, of course, determination of any taxonomic group should be based upon all parts of the animals involved, but paleontology is notoriously limited in this respect.

CONCLUSIONS

1. In the genus *Xenacanthus*, represented in this study by the Texas Permian species, *X. texensis* and *X. platypternus*, the following primitive features of the jaw and hyoid arches are apparent.

a. The mandibular knob fits into a concavity on the palatoquadrate cartilage. This condition is related to

b. The non-suspensory nature of the hyomandibular, which is indicated by the slenderness of this cartilage, its lack of articular contact with the chondrocranium, and its complete lack of any processes which might indicate a suspensory function.

c. The pharyngeohyal, which is indistinguishably fused with the epihyal to form the hyomandibular in all other known sharks, apparently persists as a distinct rudiment in the xenacanth hyomandibular.

d. The antero-posterior arrangement of the two articular facets of the joint between upper and lower jaws resembles the condition that exists in *Cladodus wildungensis*, as described by Gross.

2. Three species of *Xenacanthus* described from the midwestern Pennsylvanian, *X. compressus*, *X. latus*, and *X. gracilis*, actually represent growth stages of one species, which should be designated *X. compressus*.

3. Two species are recognized from the Permian deposits of north-central Texas. One, *X. texensis* (Cope) is restricted to the Wichita group and is closely related to *X. compressus*. The other, *X. platypternus* (Cope), is restricted to the Clear Fork group; it is descended from an unknown Pennsylvanian ancestor, not closely related to *X. compressus* or *X. texensis*. Its appearance in the Clear Fork is in all probability the result of immigration.

4. Generic distinction between *X. texensis* and *X. platypternus* is doubtful, although their European counterparts are placed in separate genera. However, the Old World forms are known in greater detail, and final decision regarding American forms should await comparison of more nearly complete material.

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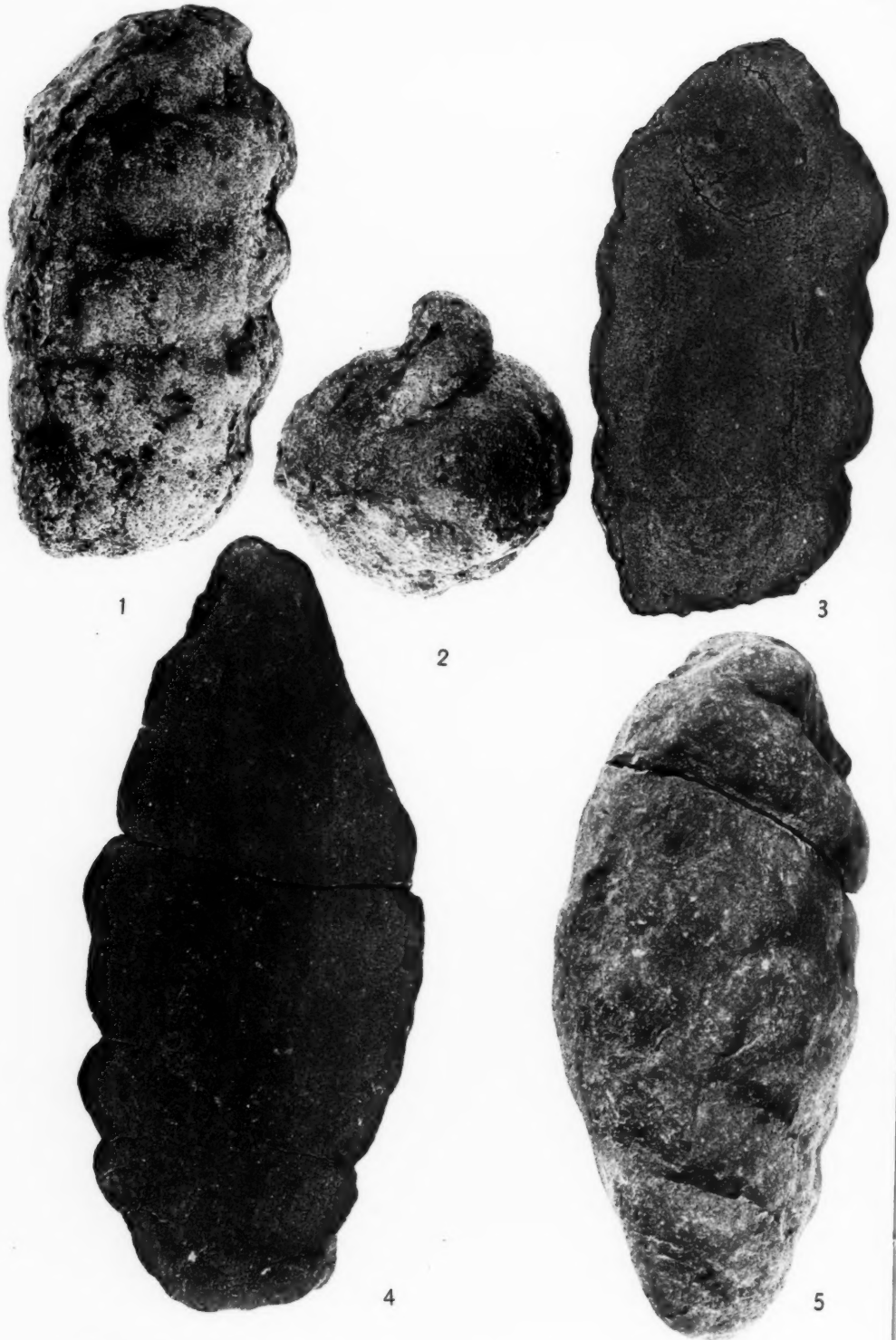
EXPLANATION OF PLATE 58

CNHM UF 113; jaw and hyoid arch elements of *Xenacanthus platypternus* ($\times\frac{1}{2}$). ac, Articular cotylus; ap, articular process; df, dental furrow; mk, mandibular knob; o, orbit; op, orbital process; p, palatine region of palatoquadrate; pr, pharyngeohyal rudiment; q, quadrate region of palatoquadrate; qc, quadrate concavity.

FIG. *1*—(A) Left palatoquadrate cartilage, external aspect. (B) Left hyomandibular cartilage, external aspect. (C) Left palatoquadrate, internal aspect. (p. 490)

2—(A) Right Meckel's cartilage, external aspect. (B) Right ceratohyal cartilage, external aspect. (C) Right Meckel's cartilage, internal aspect. (p. 491)

Hotton, American xenacanth sharks



Gilliland and La Rocque, Paleocene *Xenohelix*? from Utah

JOURNAL OF PALEONTOLOGY, VOL. 26, NO. 3, PP. 501–504, PL. 59, 1 TEXT FIG., MAY 1952

A NEW *XENOHELIX?* FROM THE PALEOCENE OF UTAH

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INTRODUCTION

IN 1947 several peculiar, regularly spiral objects of enigmatic origin were found in the southern portion of the Valley Mountains, Utah, where the objects occur in the fresh-water Flagstaff limestone of Paleocene age. The striking peculiarities of these forms, as well as their slight similarity to previously described objects from marine beds, invites description and comparison.

Occurrence.—The spiral objects, to be described later in detail, were found in float unequivocally derived from a unit of the Flagstaff limestone consisting of interfingering fluviatile and lacustrine beds. Unfortunately none of the objects was found in place; therefore, their original attitude in the strata is not known. Their general stratigraphic position is shown in the following composite section measured in the southern Valley Mountains at the west end of Bald Knoll Canyon.

	Thickness (feet)
COLTON formation:	
6. Shale, reddish brown, green, maroon, gray, variegated; interbedded with minor amounts of sandstone and limestone.	
FLAGSTAFF limestone:	
5. Limestone, gray, tan, lavender, red; colors are generally lighter than those in unit below.....	216
4. Limestone, sandstone, conglomerate, alternating beds of red, lavender, gray, yellow, mottled limestone and similarly colored beds of sandstone; a few conglomerate beds not exceeding 10 feet in thickness; the *Xenohelix?* were found in float derived from approximately the lower one-third of this unit.....	460
3. Limestone, gray mottled with pink.	296
2. Limestone, dominantly buff, gray, and yellow but mottled with pink, brick-red, and lavender; the limestone is silty and sandy; a few sandstone lenses up to 5 feet thick; minor amounts of red, green, and reddish brown shale.....	337
NORTH HORN formation:	
1. Sandstone and shale, brown, red and purple.	

The Flagstaff limestone, throughout most of its extent, is composed of gray limestone and shale, plainly lacustrine in origin. In the southern Valley Mountains, however, the typical lacustrine facies gives way to interfingering fluviatile and lacustrine littoral deposits. The lithologic unit in which the *Xenohelix?* occur is a transitional facies deposited near the fluctuating margin of the Flagstaff lake. Whether the forms in question originated in typical flood plain environments or in more typical lacustrine conditions is not known.

EXPLANATION OF PLATE 59

(All figures are natural size.)

Xenohelix? utahensis Gilliland and La Rocque, sp. nov.

FIG. *1*—External view of the holotype, O.S.U. No. 20201, showing the character of the whorls in a dextral specimen.

2—End view of a paratype, O.S.U. No. 20203, showing the diameter of the coil and its regular aspect, together with its irregular termination in a sinistral specimen.

3—Longitudinal section of the holotype, O.S.U. No. 20201, showing the outline of the whorls, the character of the central core, the plug at one end, and the diaphragms obstructing the core. Details of these structures have been drawn in text figure 1.

4—Longitudinal section of the specimen shown in figure *4*, O.S.U. No. 20202, showing the eccentric position of the tube and the diaphragms obstructing the core.

5—External view of a paratype, O.S.U. No. 20202, showing the slightly greater pitch of the spiral and the fusoid outline in another sinistral specimen.

SYSTEMATIC DESCRIPTION

XENOHELIX? UTAHENSIS Gilliland and La Rocque, sp. nov.

Plate 59, figures 1–5; text-figure 1

Description.—The whorls are multispiral, sinistral or dextral, appressed, irregularly wound around a wide central core. There is no perceptible increase in diameter of the whorls from one end of the spiral to the other. The surface is roughened by rounded elevations obscurely aligned in rows parallel to the axis of the spiral. The peripheral wall seems to be confined to the external surface of the whorls. The central core is cylindrical, wider than the diameter of the whorls, and partitioned into many chambers by numerous thin, curved diaphragms.

Measurements of type specimens

	Spiral	Length	Max. Width	Dia. of Whorl	Dia. of Core	Percent of Width	No. of Whorls
		mm.	mm.	mm.	mm.		
Holotype, OSU 20201	D[1]	81	42	15	19	45.2	5
Paratype, OSU 20202	S	103	48	14	22	45.8	8
Paratype, OSU 20203	S	76	42	10	—[2]	—	6.5
Paratype, OSU 20204	S	59[3]	43	12	21	49	6
Paratype, OSU 20205	D	44[3]	41	10	18	44	4 plus

[1] D: dextral; S: sinistral.
[2] Specimen not sectioned.
[3] Specimen incomplete.

Type Locality.—West end of Bald Knoll Canyon, section 26, Township 20 S., Range 1½ W. (Salt Lake Meridian), Sevier County, Utah. Unit 4 of section above. Flagstaff formation, Paleocene.

Types.—Holotype, no. 20201, The Ohio State University, Geological Museum; paratypes nos. 20202, 20203, 20204, and 20205, The Ohio State University, Geological Museum.

Relationships.—*Xenohelix? utahensis* differs from all previously described species of the genus in its manner of coiling. *X. marylandica*, *X.? clarki*, and *X.? mexicana* Mansfield are all loosely coiled, the several whorls being separated from each other, whereas in *X.? utahensis* they are closely appressed. Our species nevertheless resembles the genotype of *Xenohelix* sufficiently to warrant assignment to that genus, though with some doubt. *X.? utahensis* resembles the genotype in the character of its external surface which has an obscure pattern of pustules aligned more or less parallel to the axis of the coil. It differs from other Xenohelices also in the septation of the core but it is recognized that this may be due to different preservation in the several species.

Remarks.—Much has been written on the origin of *Daimonelix*, a group of objects which appear to be related to *Xenohelix*. It is unnecessary to review here the several theories advanced for their origin since this has already been done for *Daimonelix* by Schultz (1942) and for *Xenohelix* by Mansfield (1927, 1930). The finding of *Xenohelix?* in non-marine beds introduces a new factor into the discussion of its origin. Mansfield (1930, p. 1) thought that "some marine plant, perhaps a fucoid, seems the more likely" agent responsible for their origin. Marine plants must obviously be excluded in explaining the origin of organisms found in the Flagstaff, whose fauna and flora are unquestionably non-marine. On the other hand, several other possible explanations, supposing a non-marine origin, may be advanced, but each of these has been rejected by us as unconvincing. A brief review of these possibilities may be helpful in arriving at more acceptable conclusions.

Heer (1865, pp. 438, 439, fig. 326) thought that *Xenohelix*-like structures from the Miocene of Switzerland were probably filled-in borings made by some species of pelecypod. This could not be the case for the Flagstaff species for the pelecypods of the formation, Naiades and Sphaeriids, are represented by living species which are not known to construct spiral burrows.

The convincing explanation advanced for *Daimonelix* by Peterson and concurred in by Schultz (1942, p. 20) could not be applied to *X.? utahensis*. It would be difficult to find a rodent small enough to dig a burrow of this size and even the smallest shrew would find it uncomfortably narrow.

Concretionary origin must also be excluded as there is no trace of concentric structure; besides the spiral design on the exterior of the specimens is difficult to reconcile with concretions. Some concretions, from the Colton formation of the Wasatch Plateau, were formed around gastropods of the genus *Goniobasis* and show traces of spiral design in the first stages of formation, but with increase in size of the concretions the spiral design is lost. In any case, if such were the origin of these specimens, some trace of the snail which served as a nucleus should be visible, even if the snail itself had been dissolved away. The straight-walled tube inside each of the specimens seems to exclude this explanation of their origin.

One of the first explanations to spring to mind for these specimens is that they might be coprolites. Coprolites with a spiral design have been described by Case (1922, pp. 83–84) from the Upper Triassic of the Holmes Creek region, western Texas. They agree in size (length 10 to 70 mm.) with some of our specimens but differ in having a relatively smooth termination on which the spiral design is absent. Case attributes his specimens to Dipnoan fishes with some doubt. So far, few fish remains have been recorded from the Flagstaff limestone. No complete skeletons have been recorded but scales of considerable size (up to 20 mm. in diameter) are sometimes found. Judging from the fish remains of the Green River formation, with which the upper Flagstaff intertongues in places, the only fishes of sufficient size to produce coprolites of the nature of *Xenohelix? utahensis* would be the large garpike found in the Green River. There were doubtless other vertebrates of sufficiently large size living in Flagstaff time to produce such coprolites, but the central core of our specimens is still difficult to reconcile with coprolitic origin.

The central tube, size, and plugging of the tube (see text figure 1) would agree with the general structure of crayfish chimneys but modern ones are not spiral on the outside and the diaphragms obstructing the central core would seem to exclude crayfish chimneys from consideration. In addition, no remains of crayfish have yet been found in the Flagstaff. If their chimneys had been preserved, one would expect also to find remains of the animals themselves.

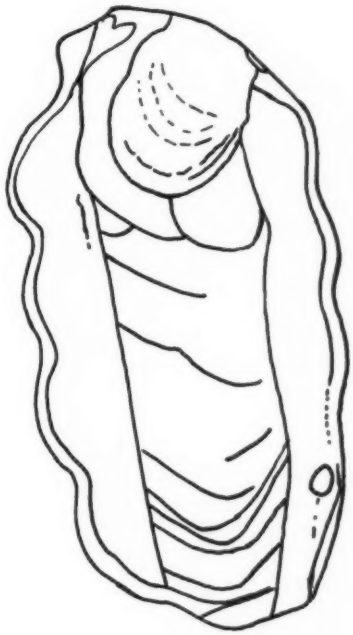

FIG. *1*—*Xenohelix? utahensis* Gilliland and La Rocque. Drawing of a section of the holotype, O.S.U. No. 20201, showing the internal structures, especially those too faint to be seen clearly on a photograph. Note the central core with the numerous, irregular diaphragms, the terminal plug and the appearance of an external wall on the whorls, probably due to oxidation of the external layer of the specimen. ×1.

Concretions formed around roots sometimes attain the size of our specimens and the central tube with its septation might be interpreted as remains of the roots around which a concretion formed, but here again, one would expect some trace of concentric structure in the outer layers of the concretion and the spiral design of the exterior would remain unexplained.

One might think of these specimens as

molds of gastropods from which all shell material had been leached away. In that case, the central tube would have to be considered as the mold of the columella. If so, the columella would not have straight sides, and there should be some trace of the outline of the whorls on the walls of the tube. Our specimens are larger than any fresh-water or land snail so far found in the Flagstaff or in any other Cretaceous or Cenozoic formation. They do not match the habit of growth of such gastropods; in particular, the "columellar tube" would be much too wide in proportion to the diameter of the whorl for any gastropod known to us. The nearest approach is found in the squat, many-whorled, stubby-spired Holospiras and Coelocentrums, but they are all much smaller than the smallest of our specimens.

To summarize, the origin of *Xenohelix* remains almost as much of a mystery as ever. Its interpretation may even be made more difficult by the finding of representatives in non-marine beds, for any theory attempting to explain their origin must take into account formation in either a marine or non-marine environment or subsequent formation after the deposition of the beds in which they are found.

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CEPHALOPODS FROM THE HARDING AND MANITOU FORMATIONS OF COLORADO

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ABSTRACT—A collection of cephalopods from the Harding sandstone of Colorado contains *Ormoceras pollacki*, n. sp. and *Kionoceras* sp. Though members of long ranging genera, these species have their closest affinities in forms of Mohawkian age. From the same formation are two species of *Utoceras*, formerly known only from the underlying Manitou, which suggests that these specimens may indicate weathering of the Manitou and redeposition of some of its materials in the Harding formation. The genus and its allies are reviewed, and it is noted that *Kirkoceras*, also of the Manitou formation, is indistinguishable from siphuncles of the genus *Clitendoceras* and is therefore regarded as a synonym of that genus. A new species of *Plectoceras* is described from the Manitou formation, and the role of the genus, as one of the few forms which pass the Canadian-Chazyan boundary with little if any change, is discussed. *Dictyorhabdus priscus*, originally described as a chimaeroid, later referred to the cephalopods, reveals structure indicating that it is a sponge of the Hexactinellida.

INTRODUCTION

THE material described in the following pages was collected by Mr. Jerome Pollack, and in part by Dr. E. A. Frederickson, largely in connection with a restudy of the invertebrate faunal components of the Harding sandstone of Colorado. I am indebted to both of them for an opportunity to study this interesting assemblage. This and the succeeding article were written while the author was at the New York State Museum, Albany, New York. The material from the Harding sandstone consisted of orthoceracones, most of which were somewhat crushed. These forms are described below as *Ormoceras pollacki* and *Kionoceras* sp. The *Ormoceras*, though a member of a very wide ranging genus, resembles most closely known species of Black River age from eastern North America. No strikingly similar forms have been found as yet in the Chazyan, but may occur there, as the Chazy limestone of eastern New York is still yielding surprises. This general stock continues into beds currently regarded as lower Trenton rather than Black River, but is not known to me from younger beds, being replaced in the late Trenton and Cincinnatian by *Treptoceras* Flower, which may or may not be a lineal descendant of this stock. The *Kionoceras*, though again a member of a wide ranging genus, can be identified in terms of a species group which the writer has reviewed elsewhere. This group contains small and usually very slender species, and appears first in the middle Chazyan, extending upward into the Black River and middle Trenton, and is represented by some somewhat larger and definitely distinctive species in the Richmondian Maquoketa shale. The Harding form, though I have not named it specifically, appears to be closely similar to Black River and Trenton species, and markedly unlike the Maquoketa forms. The known Chazyan species are not closely comparable, being smaller and much more slender.

Among the material were some small specimens which at a glance seemed to resemble rather poorly preserved individuals of the lower Canadian genus *Walcottoceras*. Closer study showed that they were not even cephalopods, but showed the cancellate network which is peculiar to the glass sponges. Amazingly, it is this form which Walcott described as *Dictyorhabdus priscus*, and referred to the Chimaeroidea. Dean (1906, p. 135) discussed this form, rejecting its chimaeroid nature, and regarded it as a molluscan form, a conclusion which had been earlier suggested by Hyatt. This form,

generally accepted as a cephalopod, shows a structure in thin section (Dean, 1906, p. 135, fig. 114) which is utterly foreign to any cephalopod, showing thick walls occupied by canals. This sort of structure is peculiar to the Porifera, and confirms the conclusion drawn from the study of the exterior.

Walcott (1892, p. 158) lists only two cephalopods from the Harding sandstone, *Orthoceras multicameratum* Hall and *Cyrtoceras* sp. *Orthoceras multicameratum*, a species described by Emmons from the Lowville limestone of New York, is a member of the genus *Murrayoceras* Foerste. I have found no *Murrayoceras* in the present collection, and it seems quite likely that Walcott's material consisted of *Ormoceras pollacki*, which is closely septate and, when the siphuncle is not exposed, bears a superficial resemblance to the Lowville species.

Two isolated siphuncles from the Harding sandstone proved to be piloceroids, and are referred to the form-genus *Utoceras*. This genus is known from three species and, as far as I have been able to learn, three specimens, all from the underlying Manitou dolomite. These forms are piloceroids, a group of cephalopods which, from present reports, are represented by one species from the middle Canadian Longview limestone of Virginia, but are abundantly represented in upper Canadian formations in Scotland, Newfoundland, Quebec, New York, Vermont, Tennessee, Missouri and Arkansas, and appear again in considerable numbers, exhibiting great diversity of form and structure in the upper Canadian of Manchuria. The single occurrence of a piloceroid in the middle Canadian is that of *Allopiloceras breve* described from the Longview limestone of Virginia. It may be that piloceroids actually had their beginning as early as middle Canadian time, though I am inclined to suspect that this particular form may easily have been derived from an upper instead of a middle Canadian horizon, especially since practically all fossils from this region have, as far as I have been able to learn, been found in residual materials. However that may be, we have nowhere in the world any indication of a piloceroid above the base of the Chazyan. My immediate reaction upon seeing these two specimens was that they must have come from the underlying Manitou dolomite. However, I am assured that these specimens were collected by Dr. Frederickson from float definitely above the contact of the Harding sandstone with the Manitou dolomite. Specimens do not move uphill by the process of creep, and there are only two ways in which these forms could have arrived in the Harding sandstone. They could have been transported by animals, probably *Homo sapiens*, or they may represent specimens which were silicified, weathered from the Manitou dolomite, and redeposited in the Harding sandstone. The first possibility I am inclined to dismiss as too improbable. I can conceive of some mischievous student throwing such specimens up hill, but it is hardly likely that such a fate could befall two of the five known specimens of the genus *Utoceras*.

The fact that the specimens are strongly silicified makes it highly probable that they are derived from the Manitou dolomite, weathered from it and redeposited in the Harding sandstone. It is, I believe, generally accepted that the silicification which characterizes many of our Canadian dolomites, occurred relatively early in geological history. I have found some evidence supporting this view in the Canadian of eastern New York. There, most of the original limestones have been altered to dolomite, but occasional unaltered lenses of limestone are found, which can be traced laterally into the dolomites. Where such a transition can be observed clearly, it can be seen that the fossils become more and more obscure until only faint shadows of their outlines remain in the dolomites, and even these may be destroyed. However, in the dolomites, and also in the limestones, occasional specimens are preserved by silica replacement, indicating that this replacement occurred prior to dolomitization.

Additional material from the Manitou dolomite was also submitted for study. This material contained one endoceroid siphuncle, which is not described or illustrated at the present time, and one fine large specimen of the genus *Plectoceras*. In the present

state of our knowledge, it is possible to distinguish most Canadian from younger Ordovician cephalopods not only specifically but generically, and indeed, only two families pass this boundary without profound modifications, the Trocholitidae and the Plectoceratidae. The Trocholitidae are recognized as being represented by different genera in Canadian and Chazyan beds, though there are certain problems involved which I shall discuss at another time. The Plectoceratidae, however present a more anomalous situation, being previously known from *Cycloplectoceras* in the Canadian, and from *Plectoceras* of the Chazyan. Foerste (1935 p. 91) set aside Black River and younger forms as *Metaplectoceras*, on the basis of the development of an impressed zone, but I have reluctantly regarded these two genera as one, because this character is certainly not constant, and no other features can be found upon which to base a good separation (Flower, 1941, p. 10). The situation was not in the least improved when Dr. J. B. Mertie found in limestones of the Seward Peninsula of Alaska, shells of plectoceroid aspect which I described as "*Plectoceras*" *sewardense*, using quotation marks for the genus because, while this form was indistinguishable from *Plectoceras* in all external and gross internal features, the connecting rings of the siphuncle showed two distinct layers and were thick. This is a feature otherwise peculiar to the Trocholitidae and Tarphyceratidae, which I have united as the order Tarphyceratida (Flower and Kummel, 1950). Miller and Kummel (1945) proceeded to erect the new genus *Alaskoceras* for this form, basing the distinction of the genus from *Plectoceras*, not upon the structure of the siphuncle, which may represent a very real difference, but upon features of coiling and cross section which are unfortunately not constant enough in the species remaining in *Plectoceras* to permit any clear separation (Flower, 1946). The whole discussion leaves the problem exactly where it was after the original description; we still do not know whether this form is a *Plectoceras* which retains primitive connecting rings as a heritage from Canadian ancestors, whether it is in itself ancient, possibly Canadian in age, or even whether it might be a homeomorph of true *Plectoceras*, but is a member of the Tarphyceratidae characterized by strong costae. Incidentally, prior to the discovery of the difference in the structure of the connecting rings, the strong costae was the only feature by which the Plectoceratidae could be separated from the Tarphyceratidae.

The present discovery of a *Plectoceras* in the Manitou dolomite makes the problem more instead of less complex. We have here no data on the internal structure of the siphuncle; indeed, the siphuncle has not been clearly observed. But we have here a form of the aspect of *Plectoceras* which cannot possibly be construed as a *Cycloplectoceras*. Embarrassingly, the stratigraphic gap separating *Plectoceras* and *Cycloplectoceras* is now eliminated, and the morphological gap is not great. *Cycloplectoceras* is distinguished by the more circular, rather than compressed cross section, the apparent closer coiling, and the appearance of ribs at an earlier growth stage. The last two differences are not as great as published descriptions and illustrations would lead one to believe, and it is to be feared that generic distinctions in the Plectoceratidae are not very profound, and that the stock changed little from its appearance in the upper Canadian to at least middle Trenton time, when the last known *Plectoceras* disappears.

The known cephalopods of the Manitou and Harding formations are briefly listed. The Manitou formation contains the following:

Plectoceras manitouense n. sp.
Cycloplectoceras sp. Ulrich, Foerste, Miller & Furnish, 1942.
Endoceras? sp.
Clitendoceras arcuatum (Ulrich & Foerste)
C. compressum (Ulrich, Foerste & Miller)
C. gracile (Ulrich, Foerste & Miller)
C. obliquatum (Ulrich, Foerste & Miller)
Manitouoceras gracile Ulrich, Foerste, Miller & Unklesbay
M. major Ulrich, Foerste, Miller & Unklesbay
Utoceras coloradoense Ulrich, Foerste & Miller
U. gleneyriense Ulrich, Foerste & Miller
U., sp. Ulrich, Foerste & Miller
Protocycloceras manitouense Ulrich, Foerste, Miller & Unklesbay
Robsonoceras manitouense Ulrich, Foerste, Miller & Unklesbay

As noted by these authors (1944, p. 14) the presence of *Robsonoceras* is suggestive of lower Canadian age, as is the associated trilobite *Leiostegium*. The remainder of the fauna contains genera which are unknown in the lower Canadian, but are known in beds of upper Canadian age, and, for the Proterocameroceratidae, middle and upper Canadian.

The Harding sandstone has yielded *Kionoceras* sp. and *Ormoceras pollacki*, forms which have their closest affinities to species of Mohawkian age in eastern North America. In addition, there was a part of a small curved cephalopod, which could not be identified, and is therefore not described or illustrated. It was a tiny portion of a phragmocone, which was probably a small portion of an oncoceroid. In addition, reported from the Harding are *Utoceras* cf. *gleneyriense* and *U. leuromurale* n. sp. If actually from the Harding sandstone, they must represent material weathered from the Manitou dolomite and redeposited.

Order ENDOCERATIDA
Family PILOCERATIDAE
Genus UTOCERAS Ulrich Foerste and Miller, 1943

Three genera of Canadian cephalopods are based upon isolated siphuncles, *Kirkoceras*, *Oderoceras* and *Utoceras*, which show all the features of endoceroid siphuncles in the broadest sense of the term. These genera are little more than form genera for isolated siphuncles. It is not evident that the walls of the siphuncles are holochoanitic as stated in the original descriptions, for the wall structure has never been observed, and indeed, cannot be ascertained from the extant material, for not only are all specimens silicified, but separation of the endosiphuncle from the rest of the shell has taken place and the septal necks, at least, are lost. Demonstration that many Canadian cephalopods of endoceroid aspect are not holochoanitic (Flower 1941, 1945) and that the slender endoceroids with short necks, the Proterocameroceratidae, are primitive and dominate middle and upper Canadian faunas, makes this difference significant.

Kirkoceras is based upon a series of slender curved siphuncles showing external annulations marking the juncture of the septa. These markings swing orad on the concave side which is assumed, and I think correctly, to be ventral, where there is sometimes evidence of contact with the wall of the shell in a slight flattening and a suppression of the annular markings of the septa. The siphuncles are circular or slightly compressed in cross section. The known species are *K. arcuatum* of the Manitou dolomite, *K. bradleyi* of the Hastings Creek formation of Phillipsburg, Quebec, *K. compressum* and *K. gracile* of the Manitou dolomite, and *K. missiquoi* (Billings) of the Hastings Creek formation of Phillipsburg, Quebec. On the basis of extant descriptions and materials, it is not possible to distinguish these forms generically from siphuncles of typical *Clitendoceras*. *Clitendoceras saylesi* Ulrich and Foerste is an endogastric endoceroid, which occurs not in the upper Canadian Fort Cassin formation, as stated, but in underlying beds of middle Canadian age, associated with a fauna characterized by *Lecanospira* and *Hystricurus conicus* (Billings) in an association allied both to that of the middle Canadian beds near Beekmantown, New York, and the Rochdale limestone of southeastern New York, which is also unquestionably middle Canadian in age. I regard *Kirkoceras* as a synonym of *Clitendoceras*, because the two cannot be distinguished.

Oderoceras is defined as a similar slender curved siphuncle, differing from *Kirkoceras* in being depressed in section, instead of circular or compressed. The species assigned to it are of upper Canadian age, including *O. depressum* from the Cotter of Tennessee, *O. sevierense* from the same region and horizon, *O. virginianum* from a Cotter horizon in Virginia, and *O.? edax* from Grenville County, Ontario. The basis for separating this genus from *Kirkoceras*, and therefore from *Clitendoceras*, is relatively slight, but as yet no *Clitendoceras* has been found with such a depressed siphuncle in place.

The third genus in this series, *Utoceras*, has been previously known from three spe-

cies, and as far as I have been able to learn, three specimens, all from the Manitou formation of Colorado. Ulrich, Foerste and Miller note that these siphuncles, large in proportion to the two preceding forms, curved, marked with oblique annuli at the juncture of the septa, are more similar to the siphuncles of *Allopiloceras* and *Piloceras* than to any other forms, but note that the siphuncles are less rapidly expanded than in *Piloceras*, but more strongly curved than *Allopiloceras*. Previously known specimens are relatively late stages of the siphuncles, which are always more slender than the initial portion in piloceroids. The differences among these genera are reduced considerably by the two specimens described below, which represent earlier stages of *Utoceras* than any previously known. These specimens, as noted in the introduction, are clearly of Manitou aspect, as the genus is thus far known only from that formation. I am assured, however, that these specimens were collected at an elevation which preclude their origin directly in the Manitou dolomite, but that they must have come instead from the Harding sandstone. If so, they clearly represent materials weathered from the Manitou dolomite and redeposited in the Harding sandstone, for nowhere in the world have piloceroid siphuncles been found in beds younger than the top of the Canadian, and all other evidence indicates strongly a post-Canadian age for the Harding sandstone. Indeed, its other cephalopods indicate a Black River rather than a Chazyan age of the Harding formation. Even though *Utoceras* is admittedly a form genus for isolated piloceroid siphuncles, it nevertheless remains a good indicator of horizons, for such forms can only be upper and possibly middle Canadian in age.

UTOCERAS cf. GLENEYRIENSE
Ulrich Foerste and Miller
Plate 60, figures 1–4

Cf. *Utoceras gleneyriense* ULRICH, FOERSTE & MILLER, 1943, Geol. Soc. America, Special Papers, no. 49, p. 53, pl. 29, fig. 1–2.

I refer with doubt to this species a siphuncle 55 mm. long which represents an earlier stage than that shown by the holotype and only known specimen of *U. gleneyriense*. It is slightly but definitely curved, faintly compressed in cross section, evidently somewhat more rapidly expanded in the apical portion than in the adoral portion. At the lowest point at which measurements can be taken, the siphuncle is 14 mm. wide and 15 mm. high. It increases in 30 mm. to 17 and 20 mm., and retains these dimensions for the next 15 mm. as nearly as can be judged. Annuli of the surface are prominent around the entire circumference of the siphuncle, sloping orad on the concave ventral side, The annuli are rather sharply elevated, separated by shallow concave interspaces, and are spaced about six in a length equal to the adoral width of the siphuncle.

At the adoral end of the specimen the endosiphocone is well displayed. Deposits are slightly thicker on the concave ventral side than on the dorsal side, but are thickened by a prominent ridge on the dorsum, which is prominent adorally, but fades out near the tip of the cone. From this one specimen it is impossible to say whether this ridge is characteristic of the species, or whether it is an adventitious structure, perhaps comparable to the commensal worms which Foerste (1933, p. 57) reported in *Centrocyrtoceras*. This interpretation is possible, but from what is already known of the startling variations which may appear normally in the form of the endocones, it is much more probable that this is a normal structure characteristic of this species. The broken apical end of the siphuncle is too extensively replaced to yield any information concerning the blades or the endosiphotube. The cone is long, unusually slender, extending 35 mm. apicad from the adoral part of the specimen. It is compressed in section, its center located about half way between the dorsal and ventral walls.

Type.—Paleontological Research Institution.

Occurrence.—From float well above the Harding-Manitou contact, north of Phantom Canyon road, near Canyon City, Colorado.

UTOCERAS LEUROMURALE Flower, n. sp.
Plate 60, figures 5–8

Associated with *U.* cf. *gleneyriense* is a second siphuncle of similar aspect which, from its fairly rapid expansion, is also a piloceroid which can be placed legitimately in the form genus *Utoceras*. It differs from the first form in the more rapid initial expansion, the marked adoral reduction of expansion, the absence of a dorsal ridge in the endocone system, a much longer and more slender endocone, the more oblique annuli of the exterior, which are broadly rounded on the concave ventral side of the siphuncle, and which fade out onto a smooth surface on the dorsal side. Irritating though it is to find it necessary to recognize so many species with so few specimens, the differences are so great as to be beyond the limit of any variation within species in our experience.

The holotype is a siphuncle fragment 60 mm. long, increasing from 14 and 15 mm. near the apical end to 18 and 21 mm. near the adoral end. Between four and five rounded annuli occur on the surface in a length equal to its adoral width. The elevated annuli are broadly rounded, never acute, with rounded rather obscure interspaces. The annuli are more strongly oblique than in the preceding species. The endocones are again thicker on the venter than on the dorsum, producing a slightly compressed endosiphocone more broadly rounded ventrally than dorsally, lacking the dorsal ridge of the preceding form, and longer and more slender. The endosiphocone extends 45 mm. apicad from the adoral end of the specimen.

As in the preceding form, the siphuncle is too extensively replaced to yield any reliable information concerning the endocones, tube or blades.

Type.—Holotype, Paleontological Research Institution.

Occurrence.—From float apparently derived from the Harding sandstone, from the same locality as the preceding form. It may be added that both specimens are heavily indurated with red limonite, which seems to be a feature of the Harding sandstone rather than of the Manitou dolomite.

Order ACTINOCERATIDA
Family ORMOCERATIDAE
(=SACTOCERATIDAE)

ORMOCERAS POLLACKI Flower, n. sp.
Plate 60, figures 9–14;
plate 61, figures 7–10

This species is known from numerous portions of phragmocones ranging up to a shell width of 29 mm., but most specimens are considerably distorted. The shell was orthoconic, straight, slender. The holotype, one of the few specimens which escaped flattening, expands from 14 and 15 mm. to 16 and 18 mm. in a length of 40 mm., nearly the entire length of the specimen. The sutures slope slightly apicad when traced from dorsum to venter. Camerae are spaced five in a length equal to the adoral shell height, and between five and six in a length equal to the width. They are little if at all more closely spaced in the latest stage known. No specimen has been observed showing crowding of the adoral camerae, consequently the size of mature shells of the species is not known, and it is possible only to say that from our present evidence the mature living chamber represents a later stage and larger proportions than any of our specimens.

The siphuncle lies ventrad of the center, and becomes increasingly eccentric as it is traced orad in the shell. The siphuncle in the holotype remains 6 mm. from the venter (measuring to the center of the siphuncle), but its distance from the dorsum increases from 9 to 10 mm. In the latest stage observed, it is 15 mm. from the dorsum and about 10 mm. from the venter.

The septa are deceptively dissimilar in curvature among our specimens, but the discordance is clearly the result of distortion which has affected the greater number of our specimens. In the least distorted specimens the curvature of the septa is gentle, the depth of the septum being slightly less than the depth of the rather shallow camerae. The greatest depth is attained near the center, and not at the point of the septal foramen, which lies well ventrad of the center of the shell.

The siphuncle, exposed in a number of specimens, presents segments which appear

to be expanded but faintly heart-shaped, an appearance which was found upon closer examination to be deceptive. Sections of some of the best specimens reveal that the segments are rounded, expanding equally from the adoral and adapical ends. The septal necks are recurved but free, and the adapical end of the connecting ring meets the next septum with an area of adnation which is as broad as the brim of the septal neck. Preservation of the interior of the siphuncle is rather poor. This is in part due to the extensive replacement which has clearly taken place, but also in a large part to the deep red color of all sections, which made it possible to obtain photographs showing relatively poor contrast between the lighter and darker areas. Most sections show an apparent lamellar lining within the siphuncle, more reminiscent of the condition of the pseudorthoceroids than of the actinoceroids, but this is, from an examination of numerous other forms, clearly adventitious. Traces of the canal system and typical actinoceroid structure can be seen in the adoral end of the specimen shown on Pl. 60, fig. 11. Our least distorted specimen, the holotype (pl. 60, fig. 12,) shows the outline of the siphuncle rather poorly; this specimen, a relatively undistorted shell, is preserved in yellow rather coarse sandy material. Upon sectioning, little color differentiation was found on the sectioned surface, and such structures as are visible were brought to their present degree of prominence by gentle etching. This process also brought out many lines and structures which represent completely irrelevant inorganic features, shows traces of the pattern of the cameral deposits, but fails to show clearly the organic deposits within the siphuncle. Another section (pl. 61, fig. 10), which proved on photography to show such little contrast between regions which were dark red to black and others which were a bright red that it has had to be considerably retouched, shows a lamellar lining of the siphuncle which is somewhat displaced in certain segments. It is clearly, however, an organic lining derived from annulosiphonate deposits, and can be paralleled in other actinoceroids, particularly *Treptoceras* of the Upper Ordovician of the Cincinnati region. The anomalies of this structure involve some broader problems which will be briefly outlined below.

Cameral deposits are well developed in the greater number of the phragmocones, and present various appearances. Plate 60, figs. 9–10 shows two views of a flattened specimen, which shows on one flattened surface some of the cameral deposits removed, though others, notably in the camerae at the apical end, have been replaced by hematite and limonite, and were not removed by solution. Plate 60, fig. 14 shows the ventral view of another specimen in which the present remaining portion represents almost perfectly a true internal mold. Cameral deposits have been removed, and the view here shows the ventral side, where such deposits attain their maximum thickness. In the center is an irregular weathered linear groove which extends to the siphuncle, and in the apical portion natural sections of a few of the segments of the siphuncle are revealed. As this phenomenon can be seen in a good number of our specimens, it indicates that the cameral deposits are massive in the midventral region and extend to the siphuncle. On the opposite side the cameral deposits are thin but still recognizable, comparable to the dorsolateral bands noted in the Pseudorthoceratidae. Plate 61, fig. 7 is superficially similar, but represents another sort of replacement. Cameral deposits are here elevated, and are replaced with limonite, while inorganic material, filling the adoral part of each camera, is softer and has yielded more rapidly to weathering. The next specimen (pl. 61, fig. 8) shows the same general result, but with a different mode of replacement, for here the cameral deposits are replaced by calcite instead of limonite. They again form the elevated parts of the weathered section. Plate 61, fig. 9 shows one of our longest specimens, a typical form, somewhat flattened, strongly replaced by limonite, but with the cameral deposits considerably removed along a region which, from the position of the siphuncle, is mid-ventral. The varying expressions of the cameral deposits in this series of specimens shows well how different these structures can appear under different condi-

tions of weathering and replacement, which has proved no small stumbling block in the general understanding of these structures.

The camerae contain perfectly typical episeptal deposits (Teichert, 1933), and their variable expression is entirely the result of different conditions of replacement and weathering.

Discussion.—This species belongs to the genus *Ormoceras* which is extremely wide ranging. The oldest forms, which I have not yet described, are found in the Chazyan. Other species extend through the Ordovician, Silurian and into the Middle Devonian, the youngest species so far known being from the upper part of the Onondaga limestone of New York. The genus may be expected to extend even higher, as it is the only actinoceroid which approaches at all close stratigraphically to *Rayonnoceras*, which is common to the late Mississippian of both America and Europe. *Ormoceras pollacki* can be delimited more accurately stratigraphically, and there can be no question but that it belongs to a group of species so far known only from the Middle Ordovician. It is unfortunately involved with a group of forms of Mohawkian age the relationships of which present some very intricate problems which have long puzzled me, and still do.

Typical *Ormoceras* has segments which are essentially circular in longitudinal section, though occasionally wider than high. The siphuncle is commonly filled with organic deposits of the same sort as those found in other actinoceroids, the structure of which has been discussed in detail by Teichert (1933). However, there are departures from this pattern both in the form of the segments of the siphuncle, and also in the character of the deposits within them. Actinoceroids with segments which are more slender than those of *Ormoceras* are set apart in the genera *Deiroceras* and *Leurorthoceras*. It is a characteristic of many, probably most actinoceroids that in the later stages of the phragmocone the segments of the siphuncle tend to become more slender, and less expanded within the camerae. In *Deiroceras*, and also in *Troedssonoceras* the segments become slender but biconvex, and this condition is held over an appreciable length of the phragmocone. In *Leurorthoceras* the segments become even more slender, and may be slightly expanded on the ventral side and essentially straight on the dorsal side. The common actinoceroids of the Cincinnati region often attain this condition, but the ontogenetic change of the segments from a condition of *Armenoceras* to *Ormoceras*, *Deiroceras* and finally *Leurorthoceras* was so gradual in these forms, that it was necessary to set them apart as a completely separate genus *Treptoceras* Flower. All of these forms are known to have deposits within the siphuncle of the characteristic actinoceroid pattern.

However, we have other cephalopods in the Ordovician which depart to some extent from this pattern. Considering first those which are quite definitely actinoceroids, there are species which are assigned, and I think, rightly, to *Ormoceras*, in which an apparent lamellar lining of the siphuncle is formed. Annulosiphonate deposits in actinoceroids may develop symmetrically, in which case they soon fill the cavity of the siphuncle in any region of the phragmocone, except for the system of central and radial canals and the perispatium. There are a few forms, however, which show a different sort of growth, the annulosiphonate deposits of adjacent septal necks tend to fuse, forming an apparently continuous lining within the siphuncle, leaving a cavity in the central part of the siphuncle. Further growth of the deposits may cause this cavity to be reduced to a central canal, but there are actinoceroids, mainly of the *Ormoceras* type, in which a large central cavity of the siphuncle persists over a rather long interval of the phragmocone, and it is such stages which are frequently found. Not many such specimens have been figured, however, and the best example of this type of structure is *Ormoceras cannonense* Foerste and Teichert (1930, p. 287, pl. 48, fig. 3A-C, pl. 58, fig. 7). Our present form is very similar to this species in structure, but differs in the somewhat different spacing of the septa, greater curvature of the septa, and in the siphuncle which lies much closer to the ventral wall of the shell. Similar deposits have been ob-

served by the writer abundantly in certain stages of the genus *Treptoceras*, which is the dominant orthoceracone of the Cincinnatian in Ohio and Indiana.

Once it has been established that the actinoceroids can produce what appears to be a continuous lining of the siphuncle, for the radial canals may be relatively inconspicuous, as can the perispatium, it becomes difficult to distinguish actinoceroids with such structure from similar structures which are developed in other cephalopods, the actinoceroid nature of which is either not evident, a matter of grave doubt, or has been completely disproven. Deposits of this sort are characteristic of the Pseudorthoceratidae, a family not known to appear prior to Lower Devonian time, and derived from the Michelinoceratidae through the Middle Silurian genus *Virgoceras*. The siphuncles in the pseudorthoceroids become cyrtochoanitic, but the early segments are always relatively slender, and frequently orthochoanitic or very nearly so (Flower, 1939). Yet in the Upper Ordovician *Orthoceras sociale* of the Maquoketa shale, segments were found which duplicate those of *Dolorthoceras*, and moreover, the same kind of lining of the siphuncle appeared, and the similarity was so great that Miller and Youngquist (1949) assigned this species to *Dolorthoceras*. It does indeed exhibit a remarkable case of homeomorphy, which would be perfect except for one feature which this study ignored completely. *Orthoceras sociale* has an ontogenetic progression from broadly expanded siphuncle segments in the earliest known stages, through segments similar to those of *Dolorthoceras*, which may become even more slender farther orad. This is the exact reverse of the ontogenetic progression of true *Dolorthoceras*, and indeed, of all of the Pseudorthoceratidae, though in that family there is a tendency in the late ephebic and gerontic portion of the camerae toward a simplification of the outline of the siphuncle, as already shown (Flower, 1939.) It is necessary to conclude that *Orthoceras sociale* is not a *Dolorthoceras* and not a pseudorthoceroid, but it still remains to be shown whether it is an actinoceroid, or whether it belongs to some other group of orthocones which develop cyrtochoanitic siphuncles.

At least one, and very possibly more than one such stock was developed in the Ordovician. There is the family Stereoplasmoceratidae of Kobayashi, which has heavy cameral deposits, and an expanded siphuncle with a lining which, while clearly organic, is not adequately known structurally as yet. To this family the writer (Flower and Kummel, 1950) tentatively added some other Ordovician genera with cyrtochoanitic siphuncles, but some of these forms are not known to have any organic deposits in camerae or siphuncle. This may of course be because only adoral portions of phragmocones, which may commonly be free from both types of deposits, have been studied in section, but there is a very real possibility that there are some such genera which lack deposits, either because they represent a completely different stock, probably of independent origin from the Michelinoceratidae, or because, as members of this same stock, they are characterized by suppression of cameral and siphonal deposits, which are first retarded in growth so that they are confined to extreme apical parts of the camerae, and may finally be suppressed altogether.

Sactoceras, based upon *Orthoceras richerti* Barrande of the Middle Silurian of Bohemia, represents a very specialized condition, and is probably best restricted to the genotype species. Here the siphuncle, as broad and as large as that of *Ormoceras* in the early part of the shell, becomes small adorally, though the segments remain circular in section, instead of becoming longer than wide as in the genera noted above. *Sactoceras* is properly confined to the Middle Silurian, and as yet I know of no American species which are typical of the genus. However, largely as the result of an old concept of the genus, as one with relatively small slender cyrtochoanitic segments, a good number of species have been assigned to the genus from the Ordovician which have segments smaller in proportion to the shell than in *Ormoceras*, and very slightly more slender segments, but in this group of forms deposits within the camerae and siphuncle have not

as yet been made evident. It is not certain even that they are actinoceroids. Such forms (see Foerste, 1932–1933) of which only a few species have been adequately described, are actually very common among Ordovician faunas, but have escaped wide notice because they prevail in small orthoconic species which have been described without the use of sections, and in species which, because of their occurrence as fragments, have not yet been described.

One more serious problem awaits final solution among the more slender orthocones of the Ordovician to which this species belongs. It is known that most actinoceroids lack slender initial stages, but begin as blunt rapidly expanding shells. This is true of our larger actinoceroids, including *Actinoceras* itself, and is true of *Ormoceras* in part. *Ormoceras allumettense* (Billings) attains in the initial 5 mm. a shell width of 12 mm., as based upon a specimen which I shall figure at another time. However, there are other species of *Ormoceras* which apparently begin life as extremely tiny slender shells. This is apparently true of our form, though one poorly preserved fragment, 7 mm. wide basally, might possibly represent a point at or near the apex of a blunt initial portion. It is certainly universally true of the Cincinnatian *Treptoceras*, that large blunt initial portions are completely unknown, and slender shells as small as 4 mm. in diameter are known. One of our most crucial unsolved questions is whether these forms of actinoceroid aspect, in some cases exhibiting siphuncles which are typical of the actinoceroids in all structural details, represent a specialized group of actinoceroids in which the initial portion of the shell is radically different, certainly very much smaller, or whether we may be dealing here with two contemporaneous groups which are almost perfect homeomorphs. The problem is stated at this time because further comment and discussion of these vexing possibilities is badly needed, as well as a critical search for new material which may perhaps contribute toward its solution.

Ormoceras pollacki happily does not show the absence of deposits or the slender or very small siphuncle which would place it in the group of species of uncertain relationship. It is happily, a demonstrable *Ormoceras*, allied to *Ormoceras cannonense*. The form of the segments of the siphuncle is also somewhat similar to *O. ferecentricum* Foerste and Teichert of the Tyrone limestone of Kentucky. Nothing is known of the interior of the siphuncle of this form. *O. josephianum* Foerste (1933) and *O. paquettense* are quite similar, but the second of these species is known to have a blunt apical end which our form lacks. These are the only species described which are quite similar in proportions to *O. pollacki*. They indicate that this species is probably Black River or early Trenton in age. Our single known Chazyan form is not strikingly similar.

Types.—Holotype and paratypes, Paleontological Research Institution.

Occurrence.—From a shaly zone near the middle of the Harding sandstone, and about 30 feet above its base. This form has been present in all localities, from the Harding Quarry, west of Canyon City, from a locality a quarter of a mile farther north, and from Twin Mountains.

Order MICHELINOCERATIDA
Family MICHELINOCERATIDAE
Genus KIONOCERAS Hyatt
KIONOCERAS sp.
Plate 60, figures 15, 16

Two flattened portions of orthoceracones represent a species of *Kionoceras* belonging to the Ordovician group of species previously outlined by the writer (Flower, 1952). The first, (pl. 60, fig. 15) 14 mm. long, increases from 9 and 5 mm. to 14 and 4 mm. in its present condition, in a length of 12 mm. indicative of an original expansion of from 7 to 8.5 mm. Camerae are closely spaced, seven in a length of 10 mm. Lirae are numerous, 18 visible on one side, separated by broader flat interspaces, and averaging four in a width of 2 mm. No finer surface markings are preserved. The second specimen, somewhat more complete and representing a slightly earlier stage, 27 mm. long, involves oblique flattening of the septa, 6 and 9 mm. at the base, 14 and 4 mm. at the adoral end. Restoration produces a shell

7.5 mm. in diameter at the base, increasing to 8 or 8.5 mm. adorally, with six camerae in a length equal to the adoral shell width. Spacing of septa and of longitudinal lirae is identical with the preceding form. The siphuncle, seen on the septum at the base, is central.

Discussion.—This species belongs to a group of small slender *Kionoceras* which range from the middle Chazyan through middle Trenton, and reappear, though represented by somewhat larger forms, in the Maquoketa shale. The Harding form, probably an undescribed species, belongs in a subgroup with slender form and shallow camerae, including *K. erraticum* of the upper Chazyan, an undescribed form from the Lowville beds at Ottawa, and *K. trentonense* Foerste from the middle Trenton of New York. Probably the last species is more closely similar than any of the others. Nevertheless, the known range of this group of forms indicates for this one a possible range of Chazyan and Mohawkian. It is hardly worthwhile to name this form from the Harding sandstone, based as it is upon specimens which are considerably flattened, and which lack the finer surface markings. Indeed, the absence of the finer surface details is the most serious lack, for specific criteria depend largely upon these features.

Figured specimens.—Paleontological Research Institution.

Occurrence.—Shaly zone in the middle of the Harding sandstone; fig. 15 is from one-fourth mile north of the Harding sandstone quarry; the second specimen is from an outcrop between this one and the Harding quarry itself.

Order BARRANDEOCERATIDA
Family PLECTOCERATIDAE
Genus PLECTOCERAS Hyatt.

PLECTOCERAS MANITOUENSE Flower, n. sp.
Plate 60, figure 17

This species is based upon a single well-preserved specimen preserving one side of a fine *Plectoceras* attaining a disc of 85 mm. The exposed surface is somewhat weathered, but the costae of the shell are still clearly defined on the living chamber which occupies the last quarter whorl of the shell. As can be seen from the illustration, the adoral quarter volution of the phragmocone shows evidence of deeper weathering, while only the impression of the exterior of the inner whorls remains, showing once more traces of the costae of the exterior of the shell. The type preserves clear evidence of only one and one-half volutions; it is impossible to say how closely coiled the early portion may have been or how wide the umbilical perforation. The last whorl lay barely in contact with the preceding whorl, clearly without any real development of an impressed zone. The extreme adoral end of the living chamber becomes free, as is so common in the mature stages of Plectoceratidae and also the Tarphyceratidae. The cross section of the early whorls as inferred from their impressions was apparently higher than wide, a condition which is clearly maintained to the adoral part of the living chamber. The whorl is rounded in cross section, the greatest width apparently at mid-height of the whorl, and the venter shows no evidence of flattening. The whorls increase in height at intervals of a half volution from 12 mm. to 20 mm. and 30 mm., the last measurement being taken at the point at which the living chamber is beginning to become free from the inner whorl. The living chamber itself has a ventral length of 90 mm., on the curving venter, the radius of which is 60 mm. adorally. The height increases from 27 mm. to 34 mm. The costae, the only surface features which are preserved, do not increase in width or distance as rapidly as the shell increases in height; as a consequence three interspaces occur on the penultimate whorl in a length equal to the shell height, while on the living chamber about five interspaces occur in a similar length. The costae, besides being more closely spaced adorally, differ from those of younger specimens of *Plectoceras* mainly in that they apparently cross the entire ventral surface without becoming weak or disappearing altogether. This and the evident lack of a distinct ventral flattening supply the only anomalous features of our present species.

A little more than a quarter volution of

the phragmocone is preserved, showing sutures which have slight lateral lobes, swing slightly orad on the venter, but are transverse dorsally. A faint bend in the suture is noticeable on the umbilical shoulder, marking a separation from the transverse condition of the dorsum to the lateral lobes. The camerae are very shallow, increasing in depth from 2.5 to 4 mm. in the length observed. Thirteen camerae occupy the last quarter volution, with a ventral length of 48 mm., while farther apicad a similar depth is maintained, though here the septa are more obscure as far as parts of the internal mold persist.

Discussion.—The closely spaced camerae, the rounded condition of the whorl, and the adoral close spacing of the costae, which apparently persist over the venter unmodified, characterize this species. None of these features seem sufficient to warrant setting the species apart in a separate genus. Ulrich, Foerste, Miller and Furnish have described and figured from the Manitou limestone as *Cycloplectoceras*?. sp (1942, p. 35, pl. 39, fig. 1) a form which is radically different from ours. The whorl increases in height much more gradually, the sutures are more widely spaced and lack lateral lobes, the costae are more widely spaced and much less strongly inclined apicad as they approach the ventral surface. The whorls, also, are much more slender in proportion to the size of the disc.

Nothing has been said of the siphuncle. No trace of it shows in the specimen. It is evidently quite close to the venter, for only the ventral surface of the phragmocone is poorly preserved and perhaps incomplete in places.

Holotype.—Paleontological Research Institution.

Occurrence.—From the Manitou dolomite, Sec. 34, Township 16 S., Range 69 W., northeast of Canyon City, Colorado.

Phylum PORIFERA

DICTYORHABDUS PRISCUS Walcott

Plate 61, figures 4–6

Dictyorhabdus priscus WALCOTT, 1892, Geol. Soc. America, Bull., vol. 3, p. 165, pl. 3, figs. 1–5.
—— DEAN, 1906, Chimaeroid fishes and their development. Carnegie Inst. of Washington, pp. 134–135, figs. 113–114.
—— BRYANT, 1936, Amer. Phil. Soc., Proc., vol. 76, p. 410.

Walcott described as the notochordal sheath of a fossil chimaeroid fish, a peculiar object from the Harding sandstone which was essentially linear, with growth lines, and spout-like processes on one side. Dean, restudying the material, came to the conclusion that they could not possibly have any connection with the Chimaeroids, and regarded them as the lip of a molluscan shell, and that it was probable that they represented portions of cephalopods. He further notes that Hyatt had commented upon the cephalopod nature of this form, but could not find the reference. Nor could the writer. Dean further made sections of this form, one of which he figures. These sections show a thick wall, perforated by tubes. The thickness and the tubular perforations are both features unlike any cephalopod, and indeed, unlike any known mollusc.

I have had two representatives of this form. The smaller and more imperfect seemed to have septa, and resembled nothing more strongly than a *Walcottoceras* in which the annuli had been suppressed on one side of the shell. Upon closer examination the septa proved to be superficial, and were the result only of extremely strongly incised growth lines. The larger specimen consisting of an internal mold covered with carbonaceous material, and an external mold, showed the processes on one side to appear as nodes rather than spout-like processes as originally figured by Walcott. The internal mold showed also growth lines, indicating that the creature grew from the narrower to the broader end. Examination of the external mold (pl. 61, fig. 4) showed a structure which at once explained the nature of this singular fossil, an interpretation which was at once corroborated by Dean's sections. This specimen shows clearly an oliquely arranged fine cancellate network, which, except for its oblique position, is the exact duplicate of the structure in the Devonian Dictyospongiae. Indeed, the presence of such a network is consistent with no other known group of organisms. Returning to Dean's figured section, the sponges are also the only group

characterized by thick walls traversed more or less completely by linear canals at right angles to the axis of the tubular organism.

The genus and species may be redefined as follows: A hexactinellid sponge, tubular, one side essentially straight, the other flared into lobes at regular intervals. On the relatively smooth side are transverse growth lines, often sharply incised and resembling septa of a cephalopod, which are weak or wanting on the lobed portion. Surface with a cancellate siliceous network, in the main, appearing as oblique to the main axis of the animal. This is produced by the flaring laterad of the longitudinal elements of the smooth side, and the transverse series is bent downward on the opposite side correspondingly. The wall in section, as shown by Dean (1906) reveals canals suggestive of the sycon type of structure, but may be actually more complex.

This form is remarkably isolated stratigraphically. Siliceous sponges with such a well established network are much younger, the majority of those known being Devonian, and in fact, Upper Devonian. We do not have eough information to place this sponge with certainty. The lobes which are here developed on one side may be comparable to those of a *Hydnoceras* or a *Ceratodictya;* on the other hand this form also displays characters in the lobes suggestive of the Titusvillidae, but our present material fails to indicate the complex organization of the titusvillid sponges. On the other hand, such walls and canals as are reported by Dean are not found in the Dictyospongiidae.

Figured specimen.—Paleontological Research Institution.

Occurrence.—From the Harding sandstone, from Sec. 34, Township 16 S., Range 69 W., northeast of Canyon City, Colorado.

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MANUSCRIPT RECEIVED APRIL 25, 1951

EXPLANATION OF PLATE 60

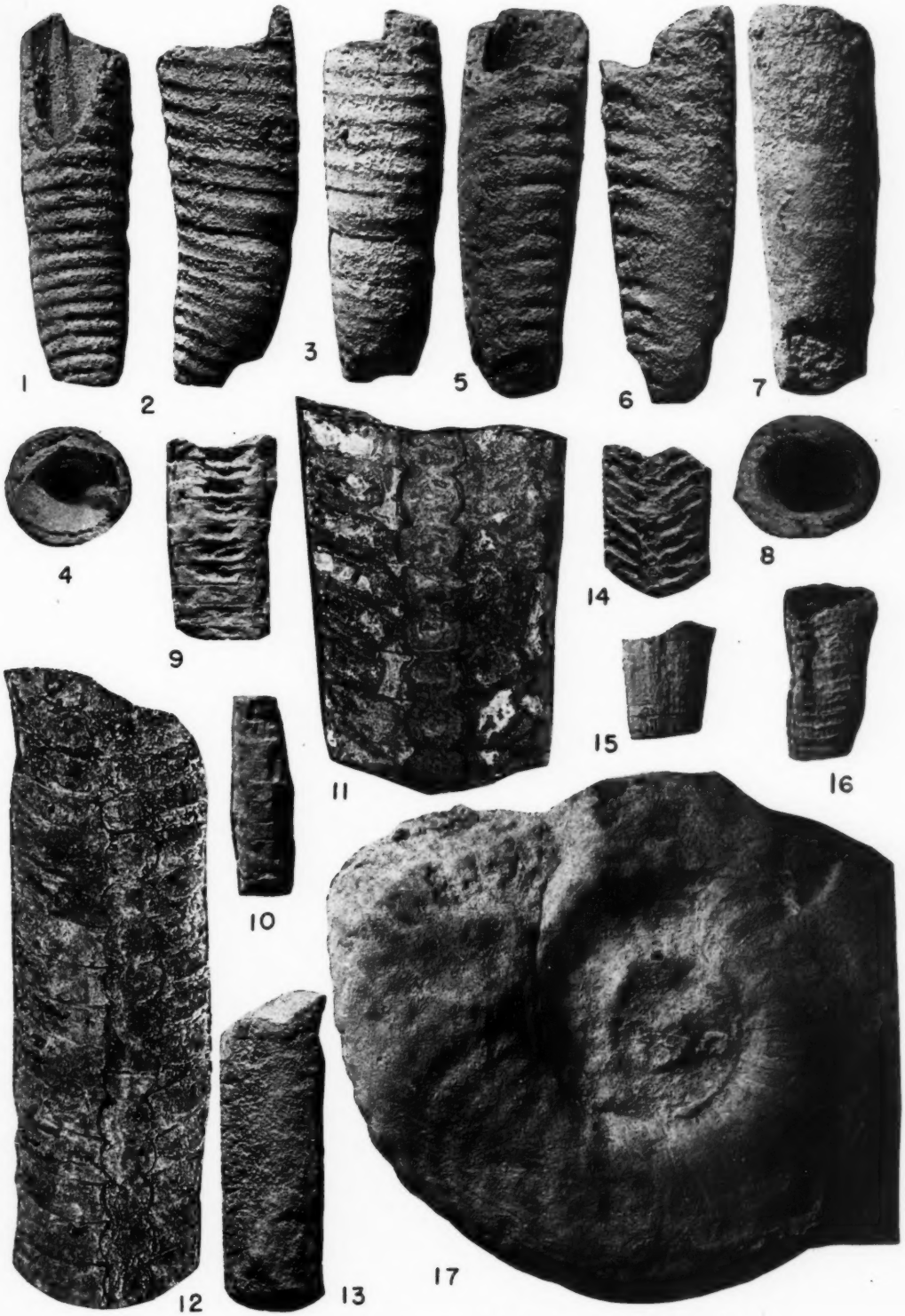
FIGS. *1–4*—*Utoceras* cf. *gleneyriense* Ulrich, Foerste & Miller. *1*, Concave, supposed ventral side; *2*, lateral aspect, venter on left; *3*, dorsal aspect; *4*, adoral view, oriented as in fig. *2*. From float well above the Harding-Manitou contact, north of Phantom Canyon road, near Canyon City, Colorado. (p. 509)

5–8—*Utoceras leuromurale* Flower, n. sp. Holotype. *5*, Concave side, supposed venter; *6*, lateral view, venter on left; *7*, dorsal view; *8*, adoral view, oriented as in fig. *6*. Same occurrence as the above. (p. 510)

9–14—*Ormoceras pollacki* Flower, n. sp. *9–10*, Two views of a flattened paratype, showing typical extent of flattening of material in the Harding sandstone. The ventral surface, shown in fig. *9* shows removal by solution of the cameral deposits in some of the camerae. Harding sandstone, Harding quarry, west of Canyon City, Colorado. *11*, Horizontal vertical section of a paratype, ×2, showing outline of siphuncle (slightly retouched), traces of cameral and siphonal deposits. The slight contrast is due to the condition of the specimen, which was a deep red and white uniform in color. Harding sandstone, one-fourth mile north of Harding sandstone quarry. *12–13*, Holotype, vertical section ×2, and exterior, ×1, of the only unflattened individual. Outline of siphuncle slightly retouched in section. Harding sandstone, one-fourth mile north of Harding sandstone quarry. *14*, Ventral view of a typical slightly flattened specimen, in which matrix has been removed by weathering, and cameral deposits stand out in relief, being replaced by limonite. Harding sandstone quarry, Canyon City, Colorado. (p. 510)

15–16—*Kionoceras* sp. Two flattened specimens, ×1, from the shaly zone in the middle of the Harding sandstone. Fig. *15* is from one-fourth mi. north of the Harding sandstone quarry; fig. *16*, from a locality between this and the Harding sandstone quarry itself. (p. 514)

17—*Plectoceras manitouense* Flower, n. sp. Holotype and only known specimen, retaining a relatively complete living chamber, somewhat weathered, but showing the numerous costae; the internal mold over the phragmocone is weathered deeper and deeper as it is traced toward the apex; only the external mold of the inner whorls is preserved, again showing traces of the costae of the surface. Manitou dolomite, Sec. 34 Township 16 S., R. 69 W., northeast of Canyon City, Colorado. (p. 515)



Flower, Harding and Manitou cephalopods

Flower, Harding and Manitou fossils; Devonian *Centroceras*

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THE ONTOGENY OF *CENTROCERAS*, WITH REMARKS ON THE PHYLOGENY OF THE CENTROCERATIDAE

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ABSTRACT—The early portion of the shell of *Centroceras marcellense* is illustrated and described. The ontogeny of the surface and cross section are reviewed in relation to possible ancestors and descendants of the genus, with frankly unsatisfactory results. The extreme early stages are regarded as coenogenetic; neanic cross section and surface features suggest a derivation from the Tetragonoceratidae, a conclusion already reached on the basis of adult features. If so, the Centroceratidae may be allied to the Rutoceratida, and the orders Centroceratida and Rutoceratida may eventually be united, though the present evidence is not strong enough to warrant such a step at the present time.

INTRODUCTION

Centroceras is a Middle Devonian genus of striking aspect, with a strongly quadrate whorl, broad across the sharp umbilical angles, narrow across the venter, with prominent lateral and ventral lobes. The family Centroceratidae was revised (Flower, 1945, Flower and Kummel 1950) to include forms with such cross sections, showing considerable variation in degree of coiling, but eliminating those genera which showed a quadrate cross section which was exactly the reverse of that of *Centroceras*, being broad across the abdominal angles and narrow across the umbilical angles. Such genera were set apart in the family Tetragonoceratidae.

The origin of the Tetragonoceratidae seems to be fairly well established on the basis of adult rather than ontogenetic features; it can be traced through forms of more rounded whorl into such genera of the Rutoceratidae as *Hercoceras;* indeed, at this point it is difficult to draw a clear line between the families, though on the whole they are quite distinct, the Rutoceratidae being more rounded in section, with broad whorls and complex ornament, the Tetragonoceratidae having the whorls typically higher than wide, quadrangular in cross

EXPLANATION OF PLATE 61

FIGS. *1–3*—Early portion of *Centroceras marcellense* (Vanuxem), Cherry Valley limestone, Middle Devonian; Oneida Creek, southwest of Stockbridge, New York. *1*, Lateral view, ×3, showing faint nepionic constriction, then appearance of ventral nodes, beginning of lateral sinus, development of angular umbilical shoulder. *2*, View of same specimen from the front, showing the first half whorl in ventral aspect, with faint nepionic constriction and inception of ventrolateral nodes. ×3. *3*, Same, ×4, slightly turned to show a later stage of the ventral face of the first half whorl, and showing more clearly the first nodes and the lirae of the ventral surface. New York State Museum. (p. 522)

4–6—*Dictyorhabdus priscus* Walcott. *4*, External mold, ×3, showing reticulate network of spicules. *5*, Internal mold, ×1; *6*, Internal mold, ×3, showing lobes and fainter growth lines. Harding sandstone, near Canyon City, Colorado, Sec. 34, T. 16 S., R. 69 W. (p. 516)

7–10—*Ormoceras pollacki* Flower, n. sp. *7*, Ventral view of a typical flattened specimen, weathered to siphuncle from ventral side. Cameral deposits and siphuncle are limonite replacements. Harding sandstone, one-fourth mile north of Harding quarry, Canyon City, Colorado. *8*, A slightly flattened specimen replaced by calcite and weathered slightly beyond the siphuncle from the ventral side. Harding sandstone, Twin Mountains, north of Canyon City, Colorado. *9*, An unusually long succession of camerae, flattened, and weathered, showing traces of cameral deposits in a much less advanced growth stage. From the Harding sandstone, one-fourth mile north of the Harding sandstone quarry. *10*, Horizontal section of a specimen almost completely replaced with red limonite. Outline of siphuncle slightly retouched, owing to faint contrast. The adoral three segments are not retouched. ×2. Same locality as the above. (p. 510)

section, and the sutures tend to develop lobes on the ventral and lateral faces. To the Tetragonoceratidae and Rutoceratidae are traceable many of the late Paleozoic genera, those at present embraced by the families Koninckioceratidae and Tainoceratidae. But other stocks remain which, if traceable to this same group of forms, show a much less definite connection.

The largest and most significant of these stocks is the Centroceratida (Flower and Kummel, 1950), a group which the writer had originally allied with the Rutoceratida, but finally separated as a distinct order, because it could not be demonstrated that the stock which began in Middle Devonian time with the genera of the Centroceratidae, could be traced with certainty to any ancestral types.

The discovery of the early stages of *Centroceras* might, it was hoped, shed valuable light upon this important problem. However, as is shown below, the early stages of *Centroceras*, though they exhibit an interesting series of changes in cross section and surface features, present evidence which is definitely ambiguous, being open to several different interpretations on the basis of recapitulation of the adult stages of older and potentially ancestral types. Yet no one of these similarities is close enough to permit one to select it as true and reject the others as false. In the end, the most logical solution seems to be to disregard the extreme early stages as either coenogenetic features, or features in which the recapitulation is so incomplete and so strongly modified that as yet it is not possible to interpret it with certainty, to point out which features are significant, and in what way they have been altered. For this reason, it seems wisest to retain, at least tentatively, the Centroceratida as an order. It is the belief of the writer that the Centroceratidae arose from the Tetragonoceratidae, and that family in turn from the Rutoceratidae, and ultimately from the Oncoceratida which appear first low in the Ordovician. The question is a significant one, for if so, a large group of coiled cephalopods which extend from the Devonian through the late Paleozoic, where, indeed, they are the most abundant and conspicuous of all nautiloid types, are derived not from the nautilicones of the Ordovician and Silurian, but from the cyrtochoanitic cyrtocones and brevicones which, under Hyatt's older classification, were considered a completely distinct group characterized by the expansion of the siphuncle within the camerae and the consequent recurved condition of the septal necks.

SUMMARY OF THE CENTROCERATIDAE

Only five genera are at present assigned to this family. *Centroceras*, the genotype, is a tarphyconic species, the whorls in contact but with no true impressed zone. The genotype, *C. marcellense* (Vanuxem) is from the Cherry Valley limestone of central New York, where it is not uncommon. The Middle Devonian of Illinois has yielded a gigantic species *C. amplum* (Meek and Worthen) described originally as *Nautilus* (*Discites*) *ornatus* var. *amplus*. Undescribed species represent the genus in the Columbus limestone of Ohio, the Jeffersonville limestone of Indiana, the Middle Devonian of northwestern Canada. The genus is as yet unknown in the Lake Winnipegosis region. In Europe the only species is *C. tetragonum* D'Archiac and de Verneuil (1842) of the Eifel Devonian, probably from the *Stringocephalus* limestone, though I have seen no specimen bearing accurate horizon data.

Homaloceras is a large cyrtoconic to gyroconic form, the whorl compressed, the dorsum rounded, the venter narrow and slightly concave. Though reminiscent except in cross section (for the greatest width is near the dorsum rather than the venter), of a stage in *Centroceras* prior to the development of the sharp angles on the umbilical shoulders, it is not possible to say whether *Homaloceras* is an uncoiled *Centroceras*, and the rounding of the dorsum is to be looked upon as a simplification, or whether *Homaloceras* is the primitive radicle. As will be seen, other evidence, largely influenced by the fact that connections are possible through *Centroceras*, but there is nothing similar enough to *Homaloceras* to be regarded as its immediate ancestor, leads to the conclusion that *Centroceras* is the more primitive of the two genera. The only described species of *Homaloceras* is from the Winnipegosis dolomite of Lake Winnipegosis, Manitoba. Restudy of the material has resulted in recognition of another spe-

cies, not as yet described. The genus has not as yet been recognized in any other region.

Strophiceras Hyatt is known only from the genotype, *Gyroceras binodosum* Sandberger and Sandberger, of the Middle Devonian of Germany. This form is clearly little more than a *Centroceras* in which the tubercles of the abdominal angles have been prolonged into costae over the ventral face, terminating in pairs of nodes flanking a narrow mid-ventral line. The cross section is essentially that of a *Centroceras*. Strangely, Hyatt originally referred this genus to the Rutoceratidae, probably because nodes and spines prevail in that family.

The Upper Devonian *Carlloceras* Flower and Caster is essentially a *Centroceras* with a slight impressed zone, and the umbilical and abdominal angles somewhat rounded. It is known as yet only from the type species.

Diorugoceras Hyatt (see Hyatt, 1894, p. 540, pl. 12, fig. 2), is known as yet only from the type species, *Nautilus planodorsatus* Portlock. This is a much more strongly involute form, of compressed quadrangular section, presaging the development of the younger Domatoceratidae.

Phacoceras (Hyatt, 1884, p. 292), based upon *Nautilus oxystomus* Phillips (not de Koninck, as Hyatt states) shows a loss of the ventral face and suppression of the ventral lobes of the sutures. A somewhat similar development from the *Domatoceras* stock, much later in the Paleozoic, is the genus *Stenopoceras*, where, however, involution is greater and the sutures are more specialized.

It is a surprising fact, which is becoming more and more definite as these studies proceed, that while the Devonian contains orthoconic and breviconic stocks allied to those of the Silurian, the coiled forms are for the most part easier to connect with their descendants in younger Paleozoic beds, than with any ancestral types in older strata. It has been shown that the Rhadinoceratida, which embrace the large smooth-shelled nautilicones of the Hamilton of New York, well known through numerous illustrations in spite of their actual rarity, are not developed from forms of at all similar aspect in the Silurian, but from slender costate shells, being traceable back to *Bickmotites* of the Middle Silurian, but only through the trochoceroid *Sphyradoceras*. *Naedyceras* and its allies are derivatives of the Oncoceratida. It now seems inevitable that the same stock must have given rise to the Rutoceratida, for not only is this conclusion favored by some structural evidence, but we have arrived at that conclusion only after searching in vain for any possible ancestor among Silurian nautilocones or gyrocones with tubular siphuncles.

All of this presents a possibility which I do not like to accept, and which I outline here in the hope that someone will be able to disprove it. The Nautilida, as at present conceived, is a group of nautilicones, dominantly rounded, smooth whorled, with the siphuncle well removed from the venter, often dorsad of the center of the shell. The earliest possible representative of this stock is the vexing genus *Potoceras* Hyatt, I say vexing, because this genus, known apparently only from one species and one specimen, is actually of unknown origin, and its assignment to the Devonian rests upon the presence of a *Martinia* in the matrix of the only known specimen, which is in the Museum of Comparative Zoology at Harvard. This stock is rare in the Mississippian, better developed in the Pennsylvanian and Permian, where it is represented by the Ephippioceratidae as well as by the simpler Liroceratidae. More specialized families dominate the Mesozoic.

Among them are some shells, as *Grypoceras* and *Cosmonautilus*, which develop on the inner whorls more angular cross sections, and sometimes nodes and costae, suggestive of the Tainoceratidae. They raise the question of relationship. Are these features which appear in the inner whorls coenogenetic, and therefore meaningless from the viewpoint of the origin of these genera? Or is it possible that in the old age of coiled stocks the whorls tend to become rounded, smooth, the siphuncle tends to move from a ventral position to one at the center, or even close to the dorsum? If so, and a reasonably good case for such a trend could be made out, is it not possible that the genera which we now group in the Nautilida may be convergent homeomorphs? The older forms may be derived from the Barrandeoceratida of the early Paleozoic; the later forms from the Tainoceratidae, which find their origin not in early Paleozoic nautilicones, but in

the cyrtocones and brevicones. Such homeomorphy is far from impossible, and while I hope that the evolution of the nautiloids will not prove to follow such a complex and perplexing pattern, the possibility is one at least deserving of attention.

DESCRIPTION OF EARLY STAGES
Plate 61, figures 1–3

The New York State Museum specimen supplying the basis of this description and the accompanying figures is a portion of a shell of *C. marcellense* describing about three quarters of a volution. This has been removed from a much more complete specimen which attains a disc of 95 mm., and contains in all a little more than one and three-fourths volutions. The living chamber is incomplete adorally, and the complete shell probably described two complete volutions. The specimen is not quite mature, showing no adoral modification of the ventral outline. Somewhat larger specimens are known, attaining a disc of 130 mm., and describing two and a quarter volutions.

The shell begins with a wide umbilical perforation, measuring 11 mm. from the initial stage across to the completion of the first half whorl. The extreme apex is concealed by matrix, which, from the fragile condition of the specimen, it did not seem advisable to remove. No evidence is supplied, therefore, to the perplexing problem of the cicatrix versus the presence of a protoconch.

In the first 4 mm. the shell is bluntly conical, rapidly expanding, and slightly curved. The rate of growth is not quite uniform, as there are two slight swellings in this interval separated by a faint constriction, and followed by a second broader and more conspicuous constriction, which is completely lateral, and which is apparently analogous to the nepionic constriction reported in other forms. In the intial part growth lines are very faint, though apparently quite regular. Very faint longitudinal elements can be detected only on the ventral surface. The growth lines are very faintly oblique, sloping apicad from dorsum to venter, but the inclination is slight, and their course is even, without the development of a distinct hyponomic sinus as yet.

Following the termination of the nepionic constriction, 4 mm. beyond the apex, the faint closely spaced growth lines develop into stronger and much more widely spaced transverse raised lirae, separated by broader flatter interspaces. They become curved on the lateral surface, sloping apicad more strongly as they approach the venter, and describing on the ventral surface a broad shallow rounded hyponomic sinus. At a point 6 mm. beyond the nepionic constriction, the venter, which has been becoming increasingly flattened, becomes separated from the lateral region by a pair of ventrolateral tubercles, the first of a series which is to persist throughout the remainder of the shell. The tubercles are well elevated, and the elevated portion of the shell is continued onto the lateral surface as vestigial costae. The transverse lirae are slightly strengthened on the costae, but are not arranged differently than in the interspaces. Beyond the third pair of costae the constriction of the ventrolateral region becomes more marked. At this point there is seen the first faint trace of a modification of the transverse markings of the lateral face, beginning as a slight geniculation at mid-height of the shell, and developing quickly into a prominent subangular median sinus, which remains prominent until well after the completion of the first volution of the shell, and indeed, persists to the latest known growth stage, though in the last half whorl it becomes less conspicuous because the lirae, which indicate the course of the aperture, later become increasingly oblique on the ventral face of the shell.

In the next 5 mm. radical changes take place in the cross section and surface markings. The ventrolateral tubercles become reduced in prominence and the ventrolateral angles of the shell become sharp, and the ventral surface faintly concave. The hyponomic sinus of the venter remains shallow and broadly curved, but the midlateral sinus becomes deep, strongly angular, and the most prominent feature of the exterior of the shell. It is developed on a faint rounded elevated ridge, with the lateral face faintly concave on either side of it. The dorsolateral (umbilical) shoulder develops rapidly to a strong angle, very narrowly rounded, and without tubercles at this stage. The narrow, well elevated transverse

lirae are replaced by more numerous, lower lirae which become immediately strongly fasciculate. This condition is reached just beyond the second break in the shell in our specimen, just beyond the completion of the first quarter volution.

The cross section has been higher than wide from the inception of the shell. At the position of the first break, just beyond the nepionic constriction, the greatest width lies dorsad of the center, the dorsal surface is arched, the venter narrower and more flattened. As the tubercles develop, the venter becomes increasingly flattened, and the greatest breadth of the shell is found at the level of the tubercles. Where the dorsolateral angles are first developed, the dorsum has widened to 6 mm., the venter to 4.5 mm., but the greatest width of the shell is at first on the mid-lateral ridges. From this point forward, the cross section changes gradually in shape, owing to the more rapid widening of the dorsal face in contrast to the ventral face, so that by completion of the first half whorl the essential features of section and ornament of an adult *Centroceras* are attained, with the exception of the dorsum.

From this point forward changes are minor. The prominent nodes of the abdominal angles have been thus far strong and are readily seen even on the internal mold of the shell. In the mature portion, these nodes have become smaller and less conspicuous externally, and the abdominal angles on the internal mold have become smooth. The sharp angular sinuses in the middle of the lateral faces are still present at the aperture, but are much less conspicuous, because the growth lines on the lateral face show an increasing tendency to slope apicad from dorsum to venter, and in the mature part of the shell the sinuses, though still recognizable, are faint and inconspicuous. The dorsolateral angles, smooth in the first three-quarters of a whorl, become more sharply angular later, and develop small spines after the completion of the first whorl, similar to those on the abdominal angles.

The dorsal face is slightly convex at the completion of the first half whorl and the growth lines are essentially transverse. Farther orad, the growth lines of the dorsum form a distinct saddle. Upon this, at the completion of the first volution, can be seen an impression of the ventral face of the beginning of the first whorl, including the fine surface markings, which are much more widely spaced at this point than the growth lines on the dorsum of the beginning of the second volution. The dorsum is scarcely concave here, and there is only the faintest concavity, which can be seen both on the exterior and on the internal mold. A half whorl later this slight concavity of the dorsum has disappeared. The dorsum is perfectly flat in the middle, in accordance with the flattening of the ventral face of the preceding whorl, shows an impression of the ventral surface of that whorl. Often enough of the ventral surface of the inner whorl is exfoliated, adhering to the outer whorl, to retain the hyponomic sinus. On either side, are small impressions of the spines of the abdominal shoulders of the preceding whorl. Where the entire shell of the inner whorl is removed, it can be seen that in this median flattened area of the dorsum, the growth lines are faint, and perfectly transverse. On either side the growth lines swing strongly orad from the umbilical angles toward the center, are faintly curved, concave orad. The dorsum is convex in cross section here though it is not distinctly divided, insofar as the cross section is concerned, into a median and two lateral areas. It becomes nearly flat and transverse only at the extreme adoral end, near the completion of the second volution.

The ontogeny of the sutures is not well displayed upon this specimen, but is known from several more fragmentary individuals. In the nepionic stage, prior to the development of the distant striae, and at about the location of the nepionic constriction, the suture bears shallow lateral lobes, dorsal and ventral saddles. With the flattening of the venter, and the development of nodes on the abdominal angles, the suture shows a slight increase in the depth of the lateral lobes, is transverse across the ventral face, and exhibits a broad saddle on the rounded dorsum.

At the inception of the umbilical angles, the lateral lobes have not deepened materially and a faint lobe is developed on the dorsum, which is as deep as that on the venter. In the next quarter volution the

sutures tend to swing orad toward the abdominal angles, the lateral lobes become more prominent, but the ventral lobe is still shallow, as is that on the dorsum. It is only in the second half of the second whorl that the ventral lobe becomes deeper than the curve formed by the growth lines and the hyponomic sinus on the venter. Lateral lobes are stronger, separated by prominent subangular saddles on abdominal and umbilical shoulders from the dorsal and ventral lobes. The dorsal lobe remains relatively broad and shallow.

The specimen upon which this description was based was collected by the writer in the Cherry Valley limestone of Oneida Creek at Stockbridge Falls, and is deposited in the New York State Museum.

INTERPRETATION

It would appear that the clearly outlined succession of stages found in the ontogeny of *Centroceras* may either duplicate the adult condition of ancestral genera, or, should the features be coenogenetic, might presage the adult condition of younger descendants of the genus. In either case, their study should contribute to the relationships of the genus. Unfortunately, we have to do here with a series of stages of such a generalized aspect that more than one set of affinities could be postulated from the evidence which they supply, and they are followed by more complex stages which are without close counterparts in either younger or older genera. It is necessary to conclude that either palingenesis or proterogenesis may be involved, but that certainly they are so highly modified that the early stages in this particular case are not open to a simple interpretation.

Considering first the older genera which we may hope to regard as potential ancestors of *Centroceras*, the earliest stages resemble quite a number of forms superficially, but none very closely. The early cross section is compressed, with growth lines sloping slightly apicad from dorsum to venter. This condition is found in the adult, and also the young of quite a number of Ordovician genera. It is true of *Barrandeoceras* of the Chazyan, which is more similar in the young than in the adult, for in the adult the whorls are costate and the venter is markedly narrower than the dorsum, sometimes subangular, and the siphuncle is subcentral. A similarity with the Canadian genus *Aphetoceras*, which, from its siphuncle, is a member of the Tarphyceratida, and not the Barrandeoceratida could also be postulated. As has been pointed out earlier (Flower, 1941), the internal features suggest that the Barrandeoceratida may be completely distinct in origin from the Tarphyceratida, an important question which has not yet been solved.

In younger Barrandeoceratida, the condition of the early stages of *Centroceras* is quite closely approximated in the loosely coiled *Paquettoceras*, which has a smooth surface, sutures with lateral lobes, and a compressed section, also in the associated genus *Centrocyrtoceras* which is different in that it is costate in the young stages, though the surface tends to be simplified in the latest growth stages. Our somewhat inadequate evidence suggests that the compressed costate condition of *Barrandeoceras* may be primitive, and that in *Centrocyrtoceras* the costae are being slightly reduced, the siphuncle takes a more ventral position, and that the smoothing of the shell is completed in *Paquettoceras*, costae being absent even in the early stages. If so, the absence of costae in the earliest stage of *Centroceras* is not a deciding factor in accepting or rejecting this relationship.

The earliest stages of *Centroceras* are, however, equally reminiscent in cross section and surface features, of the Ordovician Oncoceratida. Again the similarity is imperfect and not decisive. True, *Centroceras* has a tubular siphuncle in the adult, and there is no reason to believe that the segments are expanded in the early stages. However, this fact is not necessarily significant, for tubular siphuncles are present throughout life in most of the Rutoceratidae which, from other evidence, sprang from Silurian Oncoceratidae. Indeed, primitive genera of the family, including the Lower Devonian *Trochoceras*, *Ptenoceras* and *Roussanoffoceras*, as well as the lower Middle Devonian *Rutoceras*, retain cyrtochoanitic siphuncles with greater or lesser perfection. This problem has been discussed by the writer in a paper now awaiting publication in the Contributions of the Museum of

Paleontology, University of Michigan.

Among Silurian forms, other similarities can be seen. *Trochoceras nodosum* Barrande, a species which is typical of *Lechritrochoceras* except for the presence of nodes, and which if referred to that genus, largely because the erection of a separate genus for the species will obscure its obvious affinities and only add one more name to the already large list of nautiloid genera, is similar to the next stage, where faint costae develop and nodes appear on the abdominal shoulders. The recapitulation, if it is that, is at best imperfect, for the cross section of that species is too broad for the early stages of *Centroceras*, and the sutures fail to develop lateral lobes. Probably this resemblance is not an indication of relationship.

In the Middle Silurian of Bohemia there is also a group of smooth compressed shells, typified by *Nautilus bohemicus* Barrande, with *N. tyrannus* and *N. sacheri*, probably referable to the genus *Cumingsoceras* Flower 1950. These are shells of smooth strongly compressed coiled shells, the cross section narrower ventrally than dorsally, with good lateral lobes developed and growth lines which swing apicad from dorsum to venter. Ventral and dorsal lobes are absent, but an annular lobe may develop where the shells are coiled enough to develop a slight impressed zone. The main discrepancy found is that the siphuncle in *Cumingsoceras* is central, or very nearly so.

It is necessary to conclude that if the early stages of *Centroceras* are recapitulatory, they suggest an origin in several genera of the Ordovician and Silurian Barrandeoceratida, but in no one case is the recapitulation perfect enough to indicate a definite relationship. Nowhere in the older cephalopods have we found a clear counterpart of either the flattened venter with nodes on the sharp abdominal angle, or the prominent angular sinus lying on a slightly elevated ridge in the middle of the lateral face. With better costae and a less prominent abdominal angle, *Plectoceras* would be suggested, but as it is, the resemblance is not at all close. It is necessary to conclude that if there are recapitulatory early stages in the ontogeny of *Centroceras*, they must either represent an ancestral form which is as yet unknown, or are so modified that we cannot say with certainty which features are old, and which are new; nor can we point with certainty to a definite succession of ancestors in pre-Devonian rocks which show in the adults the succession of stages which have been observed in *Centroceras*.

Turning to younger forms, it is surprising in view of the wide variation found in late Paleozoic genera in cross section and ornament, that again no close similarities can be found. Hyatt (1894) regarded the early stages of *Centroceras tetragonum* as similar to the adults of *Temnocheilus*. The similarity is not particularly close. *Temnocheilus* has a diagonal whorl, broader than high. In the majority of the species the nodes are placed at mid-height of the whorl, and the dorsal and ventral faces are definitely convex. There are, to be sure, a few species in which the whorls have the nodes close to the venter and far from the dorsum, but they are clearly exceptional. The resemblance between *Centroceras* and *Temnocheilus* is not great, and further, *Temnocheilus* is connected by a genus as yet unnamed, with *Pleuroncoceras* of the Middle Devonian, and is regarded as a derivative not of *Centroceras*, but of the Rutoceratidae. Indeed, *Temnocheilus*, *Edaphoceras* and *Endolobus* which are closely allied, may have to be set apart as a distinct family, since they apparently represent a line developing from the Rutoceratidae independent of either the Tainoceratidae or Koninckioceratidae.

The Triboloceratidae, as interpreted broadly (Flower and Kummel, 1950) includes a series of genera, dominantly Mississippian, which range from compressed quadrangular forms, *Mesochasmoceras* and *Apheleceras*, to forms with lirate exteriors, more rounded whorls, through forms in which the whorls broaden, as in *Thrinoceras*, to those in which the section becomes extremely specialized, with a broad concave venter, and finally to forms of broadly depressed whorls, in which the lirae are confined to the lateral regions, and may disappear adorally. The genotype of *Planetoceras*, *P. retardatum* Hyatt, shows such features, and was therefore assigned tentatively to the Triboloceratidae. The concave venters and broad whorls of *Vestinautilus*, *Coelonautilus* and *Triboloceras*, represent a strikingly new feature in nautiloids, not known

before Mississippian time. The origin of this group proved something of a problem, again, on the basis of possible ancestors in the Devonian. None of these broad-whorled forms supplied any connection, and it was finally concluded that the only tenable connection with Devonian types was through *Mesochasmoceras*, which, in section and sutures, came very close to *Centroceras* and the Centroceratidae. If this is so, the progress in the Mississippian genera is essentially proterogenetic. For in such forms as *Apheleceras hibernicum* Foord and Crick dentate and spinose lirae are appearing in the early stages of a form which, in the adult, has the quadrate whorl of *Mesochasmoceras*, and one also reminiscent to some degree of the older Devonian *Centroceras*. On the basis of the Mississippian genera alone, no clear indication of the direction of the phylogeny or its relationship to the ontogeny can be ascertained; the stratigraphic range of the genera is not adequately known. From the present evidence, they seem to put in an appearance all at about the same time. However, nowhere in this group of forms is there anything similar to the early stages of *Centroceras*.

The Domatoceratidae are regarded as derived from the Centroceratidae, and indeed the main difference, the degree of involution, is bridged at least partially by some of the known genera. The relationship is clear on the basis of adult characters, but what is known of the early stages of the Domatoceratidae indicates that here also there is some specialization of the early stages which apparently does not indicate the phylogeny. Hyatt (1894) originally saw in *Potoceras*, known only from *P. dubium*, of unknown origin, but regarded as Devonian, affinities with *Endolobus*, but later (1900) assigned it to the Koninckioceratidae, along with *Domatoceras* and *Stenopoceras*. While admittedly the entire problem requires close re-evaluation, it now appears that *Potoceras* of the Devonian is probably the first of the Liroceratidae; the Domatoceratidae and Triboloceratidae are developments from the Devonian Centroceratidae, while the Tainoceratidae developed from the Devonian Tetragonoceratidae, which was developed in turn from the Rutoceratida. The family Koninckioceratidae requires careful re-evaluation, as do several of the genera belonging to other families. Indeed, there is some evidence, aside from the discontinuous stratigraphic distribution, to suggest homeomorphy among Mississippian and Permian nautiloids which have been assigned to the same genera. This is particularly likely in relatively smooth whorled forms of relatively simple section, such as *Acanthonautilus* and *Permonautilus*, *Endolobus*, *Stearoceras*, and *Planetoceras*.

In summary, while some confusion exists as to the exact relationship of some of the late Paleozoic coiled cephalopods, there is nothing in these forms which suggests closely the early stages found in *Centroceras*. Indeed, the forms which are closely allied to *Centroceras* from all other evidence, seem to develop in the Mississippian coenogenetic features in the young whorls, and may eventually prove to be one of the very few cases of valid proterogenesis in the nautiloids. If so, we cannot trace the proterogenetic trend back to *Centroceras* itself.

Close similarities of the early stages of *Centroceras* with either possible ancestors in the Ordovician and Silurian on one hand, or Mississippian or Pennsylvanian forms on the other, are very poor. It remains to consider whether anything in these stages may indicate affinities so close stratigraphically that they have not been considered thus far. The Devonian yields nothing similar in the adult to the extremely early stages, but as soon as the nodes on the abdominal shoulders of *Centroceras* develop, the section is broad ventrally, narrow dorsally, and the cross section and surface features are quite close to those of the family Tetragonoceratidae.

This family (Flower, 1946, Flower and Kummel, 1950, p. 614) has in the adult, whorls almost identical with the young of *Centroceras*, from the appearance of the ventral nodes to the point at which the umbilical angles are perfected. The only discordant feature is that the mid-lateral sinus is not developed, though there is instead a tendency to form a series of mid-lateral nodes in some genera of this family.

The genera of the Tetragonoceratidae are known from beds of just about the same age as those containing the oldest of the Centroceratidae; indeed, the two are found together in the upper Columbus limestone,

the Dundee limestone, the Winnipegosis dolomite. To be sure, there is some uncertainty involved in precise correlations, but clearly all of these types occur in an interval which is, broadly, the middle portion of the Middle Devonian, embracing beds of high Onondaga and low Hamilton ages. That *Centroceras* appears in association with its probable ancestors in the American section, is not necessarily a serious objection. Study of the Rutoceratidae, where the early stages are clearly recapitulatory, and in beautiful accord with the appearance of the genera in the European section, shows that this succession fails completely when applied to the American succession. Clearly, evolution of this family was very rapid in Middle Devonian time, and the present distribution of the faunas, particularly in America, was infiuenced by selective faunal factors, in part paleogeographic, and in part ecological, which we shall probably never be able to to evaluate with any degree of certainty.

The Rutoceratidae show a fairly orderly progression from *Ptenoceras* and *Trochoceras* in the Lower Devonian, to *Pleuroncoceras* in the *Calceola* limestone, to *Hindeoceras* in the lower *Stringocephalus* limestone, with *Kophinoceras* and *Diademoceras* in the upper *Stringocephalus* limestone. The situation is made somewhat more complex, by the development from *Hindeoceras* of other genera, among them *Casteroceras*, *Hercoceras*, and several types as yet unnamed. Yet in the American Middle Devonian this succession of genera shows practically no order, because individual genera were all long lived enough to be found in association with some of their own descendants. This is shown more fully in another work, now awaiting publication (Flower, Devonian gyrocones of Michigan).

If the *Tetragonoceras*-like stage in *Centroceras* is significant, and if it does represent recapitulation of the Tetragonoceratidae, the earlier stages cannot be significant, but must represent simplification of the extremely early part of the shell. The Tetragonoceratidae are traceable through *Wellsoceras* and *Nassauoceras* to *Hercoceras*, which is a member of the Rutoceratidae, and traceable to *Hindeoceras*. Further, this implies the ultimate origin of the Centroceratidae from the Oncoceratida.

It is recognized that the early stages of a cephalopod, or indeed any other organism may be recapitulatory, may presage the development of descendants, or may be only a simplification which has no great significance either in relation to ancestral types or descendants. In preparing the classification of the nautiloids, the writer had at first united the Centroceratida and the Rutoceratida as a single order, but finally separated them, largely because the anomalous condition of the young of *Centroceras* failed to indicate any conclusive relationship. The presence of a stage similar to the Barrandeoceratidae leaves as completely meaningless the later stage similar to the Tetragonoceratidae. On the other hand, acceptance of the *Tetragonoceras*-like stage requires that the other be dismissed as meaningless. I have accepted the latter interpretation as the more probable of the two, for the early stage approximates the Barrandeoceratidae, though it might as easily be nothing more than a coenogenetic simplification. If so, there has been lipopalingenesis, causing the omission of stages similar to the Rutoceratida, and though a similarity with the Oncoceratida can be found in the extreme apex, there is almost certainly no true recapitulation here, for no such stage has been found in either the Tetragonoceratidae or the Rutoceratidae, and very fine early stages have been available for study of several of the Rutoceratida.

This is not, however, the first time that such anomalous early stages have been found. It must be pointed out that Hyatt placed *Spyroceras* in the family Kionoceratidae because typical *Spyroceras*, and in fact *S. crotalum* the genotype, was found to have an early stage lacking annuli but possessing longitudinal markings, which seemed to recapitulate the condition of the adult of *Kionoceras*. Subsequent study showed that *Spyroceras* was a member of the Pseudorthoceratidae (Flower, 1939) having the internal structure characteristic of *Dolorthoceras*, and its ancestry was traceable back through smooth-shelled genera, *Dolorthoceras* and *Anastomoceras*, of the Pseudorthoceratidae, and back ultimately to the smooth-shelled *Virgoceras* and *Michelinoceras* of the Michelinoceratidae. *Kionoceras* is a genus of the Michelinoceratidae,

which was differentiated from *Michelinoceras* at least by middle Chazyan time.

While the probable origin of the Centroceratidae has been traced through the Tetragonoceratidae, it is recognized that the connection is not close and that there even exists room for doubt, and the presentation of alternate hypotheses. It is for this reason largely that the Centroceratida was set apart as an order of nautiloids by itself. The description of the early stages of *Centroceras* has supplied an opportunity to present the problem, with its somewhat conflicting evidence. If the Centroceratidae are thus derived, both the Centroceratida and the Rutoceratida, which comprise the bulk of the late Paleozoic and early Mesozoic genera of coiled cephalopods, sprang not from the coiled forms of the earlier Paleozoic, but from the Oncoceratida, a group of forms which in the Ordovician and Silurian, had cyrtochoanitic siphuncles frequently supplied with elaborate actinosiphonate deposits. That this origin is true for the Rutoceratida now seems an inevitable conclusion. It may prove true for the Centroceratida as well, but the evidence of a close connection is not yet adequate, The best taxonomic expression for this situation seems to be the recognition of the Rutoceratida and Centroceratida as separate orders.

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PALEONTOLOGICAL NOTES

A NEW MATERIAL FOR THE PALEONTOLOGIST

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A plastic impregnated fabric known as Celastic has recently appeared on the market. When dipped for five seconds in its solvent it becomes limp and strongly adhesive. It can then be bent, pushed or twisted into nearly any shape, setting into a hard, tough, almost indestructible film in fifteen minutes.

Its most obvious use to paleontologists seems at the moment to be as a protective jacket for small jaws, skulls, and other bones in field work. It can be cut into strips and laminated upon itself to form a strong, light, quicksetting jacket. While the manufacturer recommends dipping the material, it softens equally well when the solvent is flowed over both surfaces with a brush. When one is on foot in the field it is not practical to carry quantities of plaster of paris and water. However, a pocketful of Celastic strips and a pint of solvent do not represent prohibitive weight or bulk, and offer the possibility of collecting fragile specimens without extra trips back to camp. Savings in shipping weight are considerable, as is bulk if you transport your collection in your car or truck. The Celastic is readily resoftened by the application of more solvent, and specimens can be freed from their jackets without the jarring of hammer and chisel.

Another application of Celastic is as a substitute for laminated papier maché in strengthening or restoring large specimens or restorations. It dries so rapidly that work which would require weeks or months with papier maché can be done in a matter of days. It can also be used to make strong light armatures and manikins as bases for modeling restorations, and for the rough groundwork of small dioramas.

Celastic is available from Ben Walters, Inc., 125 W. 26th Street, New York 1. A brochure describing its use and applications is available on request to the company.

THE TAXONOMY AND PALEOECOLOGICAL SIGNIFICANCE OF PEMPHIGASPID TRILOBITES

PAUL TASCH
State University of Iowa

Recently the trilobite genus *Pemphigaspis*, was redescribed (Palmer, 1951, Jour. Paleontology, vol. 25, pp. 762–764). Since material previously described and figured (Tasch, 1951, Jour. Paleontology, vol. 25, pp. 294; 302; plate 46, figs. 10–11; plate 44, figs. 11–12) provides information not included in the redescription of the genus, brief mention is given here.

Apparently, there are hallaspid cranidia with "brims narrow, present only in front of fixed cheeks" as in all the specimens upon which the redescription is based, and those described by the writer, which have a brim "thinning out from either side of the anterior portion of the glabella to the medial region where it appears as a narrow depression." The latter brim also terminates in a distinctive border.

In a supplementary description of the genus *Pemphigaspis*, the writer suggested (p. 302) that the variance in elevation of the lateral lobes of the pygidium, above or below the axis, constituted a character of specific value. A new species, *Pemphigaspis intermedia* was set up on the basis of this character. Thus, the redescription of the genus should be expanded to include the above information.

Since no complete pemphigaspids, com-

plete with hallaspid-type heads as well as thoracic-pygidial segments, have been figured or described, Palmer's designation of the cranidia of *Hallaspis* as pemphigaspid heads is inferential since it is based upon the occurrence together of the respective heads and tails in beds limited to narrow or single zones in Minnesota, Texas and Montana. If this inference is correct, the reconstructed *Pemphigaspis* seems to bear out a supposition made by the writer while studying some pemphigaspid tails.

The smooth, oval, water-wing shape of the pygidium, unique among trilobites, appeared to represent a fusion of all pleural segments while the axial lobe remained unfused. In other words, caudalization was incomplete in a way that seemed to indicate an adaptation to facilitate greater buoyancy. This supposition could not be pursued further at the time. However, it can now be supported by reference to characteristics of the cephalon. The swollen anterior portion of the hallaspid head and projection of the glabella beyond the "abbreviated brim" taken together with characteristics of the pygidium, may relate to an adaptive trend away from a benthonic existence towards a quasi-planktonic or neritic-planktonic existence. Similarly, the "complete brim" and its marginal border, which terminates by curving forward, may correspond to a stage transitional between these two types of environments.

In brief, the assignment of hallaspid heads to *Pemphigaspis* appears to be supported, independent of other evidence, by a consideration of the paleocological significance of pemphigaspid cranidial and pygidial morphology.

JOURNAL OF PALEONTOLOGY, VOL. 26, NO. 3, PP. 531–532, MAY 1952

NOMENCLATURAL NOTES

MEDISTYLUS, NEW NAME FOR *PHANOPHILUS* AMEGHINO, NOT SHARP

R. A. STIRTON
Museum of Paleontology, University of California

The new name *Medistylus* is proposed for a mammalian genus of the order Notoungulata and the family Interatheriidae. Ameghino (An. Soc. Cien. Argentina, vol. 55, p. 202, 1903.) described isolated upper molars as representing a new genus and species which he called *Phanophilus dorsatus*. At that time he placed it in the family Protypotheriidae now listed in the synonymy of Interatheriidae. The name *Phanophilus* was preoccupied by Sharp (Scien. Trans. Roy. Dublin Soc., ser. 2, vol. 3, p. 380, 1886.) for a genus of Coleoptera from New Zealand. The mammalian name will now appear as *Medistylus dorsatus* (Ameghino).

FIG. 1—*Medistylus dorsatus* (Ameghino), upper molar of holotype, occlusal and labial views. Natural size. After Ameghino.

Medistylus, one of the smallest interatheres known from the Deseado late Oligocene of Argentina, differs from all the other genera in the development of a prominent mesostyle on the ectoloph. No specimens other than the type materials have been recorded, and it is not clear how many of the original teeth were available to Ameghino.

NOTICE ISSUED BY THE SECRETARY TO THE INTERNATIONAL COMMISSION ON ZOOLOGICAL NOMENCLATURE

Zoologists and palaeontologists are reminded that at Paris in 1948 the Thirteenth International Congress of Zoology decided that a number of general problems of great importance involving the text of the International Code of Zoological Nomenclature should be brought forward for decision at the next (Fourteenth) International Congress of Zoology to be held in Copenhagen in 1953. The Paris Congress further decided that, as a preliminary to the submission of these problems to the Copenhagen Congress the Secretary to the International Commission on Zoological Nomenclature should confer with interested specialists and, having done so, should submit comprehensive Reports, with recommendations.

In pursuance of the duties so entrusted to me, I have prepared papers on each of the problems remitted to me for Report, in each of which I have set out the issues on which, as it appears to me, the Copenhagen Congress will need to take decisions. In these papers also I have submitted for consideration a number of suggestions based upon such preliminary consultations as it has already been possible to hold. The object of these papers is to elicit expressions of opinion on the issues involved from as wide a circle as possible of interested specialists.

The subjects dealt with in the papers referred to above are the following:

(1) Emendation of zoological names: proposed substitution for Article 19 of simple clear-cut rules capable of being easily applied (Commission's reference Z.N.(S.)356);
(2) Clarification and amplification of the rules relating to the naming of families and lower categories of suprageneric rank (Commission's reference Z.N.(S.) 357);
(3) Proposed introduction of rules for regulating the naming of Orders and higher taxonomic categories (Commission's reference Z.N.(S.)360);
(4) Species to be accepted as the type species of a nominal genus, the name of

which was published in a generic synonymy, if names so published are to be treated as possessing nomenclatorial availability (Z.N.(S.)387);

(5) Application to be given to a trivial name which, when first published, was applied to a particular species or specimen but which is stated also to be a substitute name for some previously published name (Commission's reference Z.N.(S.) 361);

(6) Neotypes: question whether this class of type specimen should be officially recognized and, if so, under what conditions (Commission's reference Z.N.(S.)358);

(7) The means to be devised for securing stability in zoological nomenclature (Commission's reference Z.N.(S.) 359).

A special volume (vol. 7) of the *Bulletin of Zoological Nomenclature* has been allotted for the publication of the foregoing papers, which it must be understood constitute an important instalment of the Agenda on nomenclature questions of the Copenhagen Congress next year. Parts 1/2 containing the first instalment of the above papers will be published on 25th February 1952; the whole of the remainder of the volume will be published within the next six weeks.

The object of the present notice is to draw attention to arrangements being made for the consideration of the foregoing problems by the Copenhagen Congress and to express the hope that Nomenclature Committees of museums and other scientific institutions and also as many individual specialists as possible will furnish as soon as possible answers to the questions specifically asked in the concluding paragraph in each of the seven papers enumerated above regarding the action which, in their opinion or, in the case of Committees, in the opinion of their members, it is desirable that the Copenhagen Congress should take on each of the important problems involved. It is particularly hoped that there will be a wide and representative response to the present appeal, so that the proposals to be submitted to the Copenhagen Congress may be such as will command the widest possible measure of support among the general body of zoologists and palaeontologists, both those engaged on taxonomic work and also those engaged in the teaching of zoology and geology and those working in the various fields of applied biology.

Nomenclature Committees and individual specialists who respond will render a double service if they will assist the International Commission by observing the following procedure when furnishing statements of their views: (1) Where comments are furnished on two or more of the general problems enumerated above, the comments furnished on each of those problems should be on separate sheets of paper. (2) Every comment furnished should be clearly marked with the Commission's Reference Number as indicated in the list given above. (3) Comments should be typewritten, on one side of the paper only, with wide margins and should be furnished in duplicate.

In order that there may be sufficient time to prepare the Reports called for by the Paris Congress—and thus to make those Reports available well ahead of the Copenhagen Congress—it is particularly hoped that Nomenclature Committees and individual specialists responding to the present appeal despatch their comments as promptly as possible. They should in any case reach me not later than 31st July 1952.

All communications relating to the foregoing matters should be addressed to myself, as Secretary to the International Commission on Zoological Nomenclature (28 Park Village East, Regent's Park, London, N.W.1., England).

FRANCIS HEMMING
Secretary to the International Commission on Zoological Nomenclature

20th February, 1952

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SOCIETY RECORDS AND ACTIVITIES

NOMINATIONS FOR MEMBERSHIP

In accordance with Article 3, Chapter 1, of the By-Laws of the Paleontological Society, the Secretary submits the following nominations for membership in the Society. They have been approved by Council.

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IN CELEBRATION OF THE SEVENTIETH BIRTHDAY OF CORRESPONDENT RUDOLF RICHTER

On November 9, 1951 Prof. Rudolf Richter, Correspondent of this Society, celebrated his seventieth birthday, and his retirement as Director of the Senckenberg Natural History Museum in Frankfurt a.M. On December 12th, a German colleague reports a festive meeting of the Natural Science Faculty of the University of Frankfurt to which the directorate of the Senckenberg Natural History Society, Dr. Richter's many students and distinguished guests were invited. Prof. R. Brinkmann, who is scheduled as Dr. Richter's successor in the directorship of the Museum, gave the festival address on the broad field of scholarship represented in the works of Dr. Richter. Dr. G. Solle presented Dr. Richter with a copy of an impressive Festschrift which had been prepared by his students in his honor. Professor Solle and Dr. Herta Schmidt assembled the series of monographs in the Festschrift. Dr. Hoppel gave Dr. Richter the gold plaque of honor of the Paleontologische Gesellschaft, a distinction only awarded once previously.

All the speakers stressed the great scien-

tific accomplishment of Rudolf Richter in the geology and paleontology of the Paleozoic. Of no less significance was his founding and direction for many years of his research institute in Wilhelmshaven for the study of recent phenomena of geologic significance, a unique undertaking. For decades Richter's work has been characterized by the highest precision in scientific technique and a quality of integration seldom encountered in geological-paleontological researches.

On the completion of his seventieth year, the German Geological Society awarded Rudolf Richter the Hans Stille Medal, and the Paleontologische Gesellschaft made him an Honorary Member. The Paleontological Society sent Correspondent Richter a congratulatory telegram.

The Secretary has recently received a copy of the Richter Festschrift, and will review this monumental series of monographs in a succeeding number of the Journal of Paleontology. However, members of the Society may well appreciate a preliminary note on the contents and cost of the volume:

Festschrift zum Siebzigsten Geburtstag von Rudolf Richter, edited by Herta Schmidt and Gerhard Solle (Abh. senckenb. naturf. Ges., Bd. 485, pp. 1–336, 54 pls., 3 maps, Frankfurt a.M., Nov. 1951). There are 11 papers as follows: *H.-J. Lippert*, Zur Gesteins- und Lagerstättenbildung in Roteisenstein-Gruben des östlichen Dill-Gebietes, with 10 pls.; *W. Simon*, Untersuchungen im Paläozoikum von Sevilla (Sierra Morena, Spanien), with 4 pls.; *S. Simson*, Some solved and unsolved problems of the stratigraphy of the marine Devonian of Great Britain; *E.-E. Hotz and K. Krömmelbein*, Das "Antoniusbusch-Profil" im Devon der Rohrer Mulde (Eifel), 1 pl.; *R. Kräusel*, Der tertiäre "Riesenahorn" *Banisteriacarpum* nov. gen. Die systematische Stellung von *Acer giganteum* und *Acer octopterix* Göppert, with 3 pls.; *W. Kegel*, Diskordanz der Schalen bei Pectiniden und Pteriiden; *E. Triebel*, Einige stratigraphisch wertvolle Ostracoden aus dem höheren Dogger Deutschlands, with 6 pls.; *Herta Schmidt*, Das stropheodonte Schloss der Brachiopoden, with 2 pls.; *G. Solle*, Geologie, Paläomorphologie und Hydrologie der Main-Ebene östlich von Frankfurt a.M., with 1 pl. and 3 maps; *W. Schäfer*, Fossilisations-Bedingungen brachyurer Krebse, with 2 pls.; and *H. Bartenstein and E. Brand*, Mikropälontologische Untersuchungen zur Stratigraphie des nordwestdeutschen Valendis, with 27 pls.

The Festschrift is available at the *Senckenbergische Naturforschende Gesellschaft, Senckenberg-Anlage 25, Frankfurt a.M., Germany*. It is priced at DM 48., bound in linen,—or about $12.00, at current exchange rates.

JOURNAL OF PALEONTOLOGY, VOL. 26, NO. 3, PP. 535–536, MAY 1952

NOTICES

AVAILABILITY OF U. S. GEOLOGICAL SURVEY TECHNICAL FILES IN PALEONTOLOGY[1]

BY MEMBERS OF PALEONTOLOGY AND STRATIGRAPHY BRANCH, U. S. GEOLOGICAL SURVEY

Certain objective technical files of the U. S. Geological Survey's Paleontology and Stratigraphy Branch have been released as Open File Reports, and arrangements have been completed whereby either microfilm or paper facsimile copies may be purchased at cost of reproduction by interested members of the public.

Positive microfilm or paper facsimile copies of the indexes and bibliographies in question may be obtained at the approximate prices listed below, on filing of prepaid order with Mr. Jerome Kilmartin, Chief of the Map Information Office, U. S. Geological Survey, Washington 25, D. C. Checks should be made payable to The Treasurer, U. S. A. The work will be performed by the U. S. Naval Records Management Center on a cooperative repay basis, and it advises that charges are based on current materials and labor costs, and will be subject to change without notice. For this reason the prices outlined below cannot be guaranteed, and subsequent upward revision may be called for.

The available indexes are given no special authorship credit as they represent the product of Survey teamwork over a long period of time. It is further to be noted that no guarantee of their accuracy is made, as they consist primarily of uncritical compilations, in large part brought together by clerical help, and commonly not checked as to accuracy or consistency of usage. On the other hand, these records are extraordinarily useful research tools, in competent professional hands, and they are being made available to the profession at large in recognition of the fact that they have been compiled at public expense and that it is virtually impossible to bring them into shape for publication as critical indexes within the foreseeable future. The available indexes, number of microfilm rolls and images, and prices are as follows:

Compendium of paleobotanical species
(28 microfilm rolls; 135,490 images)

1. Duplicate 16 mm. microfilm	$ 56
2. Paper facsimile in continuous roll 5″ wide	1,017
3. Paper facsimile cut to consistent size	1,313

Paleobotanical bibliographical index
(5 microfilm rolls; 17,356 images)

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Mesozoic species index—North and Central America, including the Caribbean
(8 microfilm rolls; 25,459 images)

1. Duplicate 16 mm. microfilm	$ 16
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3. Paper facsimile cut to consistent size	378

Mesozoic species index—South America
(3 microfilm rolls; 8,345 images)

1. Duplicate 16 mm. microfilm	$ 6
2. Paper facsimile in continuous roll 5″ wide	109
3. Paper facsimile cut to consistent size	141

Cushman catalog of Foraminifera
(33 microfilm rolls; 118,967 images)

1. Duplicate 16 mm. microfilm	$ 66
2. Paper facsimile in continuous roll 5″ wide	1,198
3. Paper facsimile cut to consistent size	1,550

The above records will be available at prices listed, or higher, for orders placed up until the end of 1953, unless contract arrangements are sooner terminated by the Navy Department. Meanwhile, the original records and subsequent additions to them will remain available to qualified persons in the Survey's offices in the U. S. National Museum, and with the Museum's "Cushman Collection."

Other technical records of the Survey's

[1] Publication authorized by the Director, U. S. Geological Survey.

Paleontology and Stratigraphy Branch on file in its offices at the U. S. National Museum and available for inspection and use by qualified visitors, but not available for duplication and sale, are as follows:

Cenozoic card catalog and bibliographies (incomplete and in revision)	131,400	cards
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Diatom species index	40,000	"
Ostracode species index	6,000	"
Conodont synonymy index (a subjective index)	5,200	"

REPRINT COPIES OF SYMPOSIUM

Separate copies of the "Symposium on distribution of evolutionary explosions" printed as part of this issue are available in paper covers at a postpaid price of $2 each for single copies, or $1.75 each in lots of five or more. Prepaid orders should be addressed to the Secretary of the Paleontological Society, Dr. Kenneth E. Caster, Department of Geology and Geography, University of Cincinnati, Cincinnati 21, Ohio.

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Units 1-8 (Vol. I) and 9-10 (Vol. II) are still available in short supply.

STUDENT SET OF SELECTED STRATIGRAPHIC GUIDE FORAMINIFERA

In response to several suggestions, a special student set of Guide Fossil Foraminifera is being readied for publication in time for the 1952 Fall term of American universities and colleges.

This set is being compiled on the basis of a questionnaire sent to a number of university geology departments, whose replies will guide the selection of species to be included. The student set will consist of from 50 to 200 cards, depending upon final results. Any teacher of micropaleontology who has not gotten a copy of the questionnaire is cordially invited to send for one in order to insure that his views will be included in the compilation study. Deadline for replies to the questionnaire is July 15, 1952.

Those interested in further details are invited to write for particulars.

James D. McLean, Jr., P.O. Box 916, Alexandria, Virginia, U.S.A.

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BIBLIOGRAPHY OF OTOLITHS, by Robert B. Campbell, 32 pp. (Sept., 1929) ..... $1.00 per copy.

TURBIDITY CURRENTS AND THE TRANSPORTATION OF COARSE SEDIMENTS TO DEEP WATER, A Symposium, 107 pp. (Nov., 1951) ..... Non-members, $2.75 per copy
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